Vol. 17 No. 10

December, 1951

THE BOTANICAL REVIEW

Interpreting Botanical Progress

Histo-Physiological Gradients and Plant Organogenesis (Part II) ..... Henri Prat 693

FUTURE CONTENTS ON INSIDE BACK COVER

Published Monthly except August and September at
111 E. Chestnut St., Lancaster, Pa.

Entered as second-class mail matter February 4, 1935, at the Post Office at Lancaster, Pennsylvania, under the Act of March 3, 1879.

THE BOTANICAL REVIEW

Founded in 1935 by
HENRY ALLAN GLEASON and EDMUND H. FULLING
Managed, edited and published at
The New York Botanical Garden
by
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Articles are obtained primarily by invitation. Unsolicited manuscripts are also welcome. In all cases, however, the editor reserves the right to accept, reject or suggest revisions in submitted material. All manuscripts should be on double-space typewritten pages, with references and citations in accordance with the customary style of THE BOTANICAL REVIEW.

Missing numbers can not be supplied unless notice is received within two months after appearance of issues concerned.

All correspondence should be addressed to THE BOTANICAL REVIEW, at 111 E. Chestnut St., Lancaster, Pa., or Fordham P. O., New York, N. Y.

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Volume XVII
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THE SCIENCE PRESS
LANCASTER, PA.

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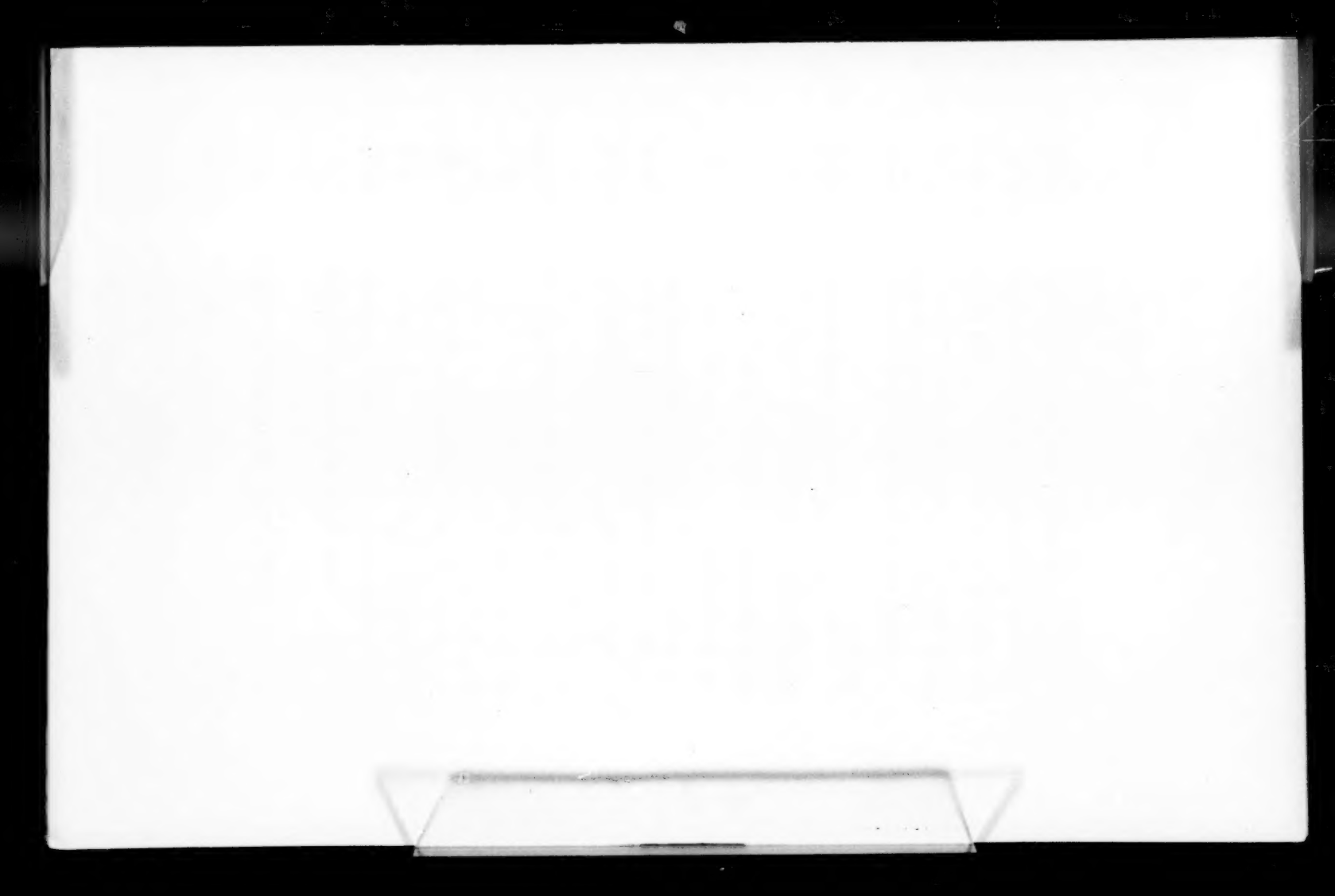

THE BOTANICAL REVIEW

VOL. XVII DECEMBER, 1951 No. 10

HISTO-PHYSIOLOGICAL GRADIENTS AND PLANT ORGANOGENESIS (Part II)

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CHAPTER V. HISTOLOGICAL GRADIENTS

In the first part of this work[1] a conspectus of facts has been given concerning, first, physico-chemical gradients in plant organisms, e.g., ionic, redox and hydration gradients; then physiological gradients, such as gradients of metabolism and of resistance against parasites, finally, growth gradients, including rate of mitosis, cell-elongation and cell-maturation. Now we shall examine the final result, the building of the plant body, with all the types of gradations inscribed in its structure. For this purpose we shall first take an example clearly showing the graded distribution of different cell types.

Distribution of Epidermis on a Grass Leaf

In Chapter IV (210, Fig. 6) the building process of epidermal cells in a grass has been described. These cells are not distributed at random but are associated according to precise laws (67, 200, 209). The most highly differentiated epidermis is built on the silico-suberous type, i.e., of siliceous (S) and cork cells (Z) in couples alternating with long ones (l_3) and surrounded by cor-

[1] While this first part (210) was in press, a symposium was held in Washington, D. C., in connection with the Botanical Society of America and AAAS meetings, on the special subject of gradients in plants (Sept. 11th, 1948). The number and qualification of participants were a good indication of the interest now taken by an increasing group of biologists in this fruitful field of research, opened half a century ago by the works of Boveri (14) and widely enlarged by the discoveries of Child concerning animal embryogenesis (20). Also encouraging was the number of letters received from all parts of the world soon after publication of Part I of the present article. To all these correspondents I extend my cordial thanks. I am specially grateful to Dr. G. L. Church, from Brown University, who kindly revised this text.

rugated walls (rippled cells) (Fig. 15, VI). The less differentiated (homogeneous) type is formed of plain cells (l_2) built on a uniform pattern, all elongated and surrounded by thin straight walls[2]. Between these two extremes an intermediate category (exodermic type) is characterized by protuberant cells—hairs, spicules, prickles, etc. (P, P_1, P_2)—alternating with flat long ones (67, 209).

Relationships between these three epidermal types are perfectly constant. They are always juxtaposed in the same order, in the way spectrum colors follow one another in an immutable sequence through all interference phenomena. For instance, taking the upper leaf from a barley plant (Fig. 15, II), we find, on the outer face of the sheath, an epidermis belonging to the silico-suberous type with strong walls (SZ l_3) and representing a prolongation of the type that covers the lower internode. It extends on to some parts of the blade, advancing in narrow bands along the bases of the principal veins.

On the blade, however, this epidermal type is not the only one present. On the veins, past the silico-suberous region, are big prickles (P_2), turned upwards. On the bands between the veins (interveinal stripes) some cell-rows are provided with spicules (P_1), hairs (P) and stomata (X), and alternate with other rows (ol_2) deprived of short cells. This arrangement is found repeated on each vein, on the inner as well as on the outer face of the blade.

The inner face of the sheath, which tightly embraces the internode, possesses a very simple structure (Fig. 15, I). Its epidermis is nearly homogeneous everywhere, consisting almost entirely of long cells with thin straight walls, among which only a few stomata (X) and small spicules (P_1) are intercalated.

This distribution is shown in the diagrams of Fig. 15 (I and II) which we call "dermograms" (74, 209). On them the silico-suberous type of epidermis (SZ) is indicated by hatchings and the exodermic one (P) by dots, the larger as the prickles grow bigger. Finally, the homogeneous type remains white (ol_2). In sections the most differentiated types of epidermis are shown by thicker strokes (Fig. 15, III, IV, V, VIII).

[2] This type is represented by the symbol ol_2, the letter o indicating absence of specialized elements (short cells).

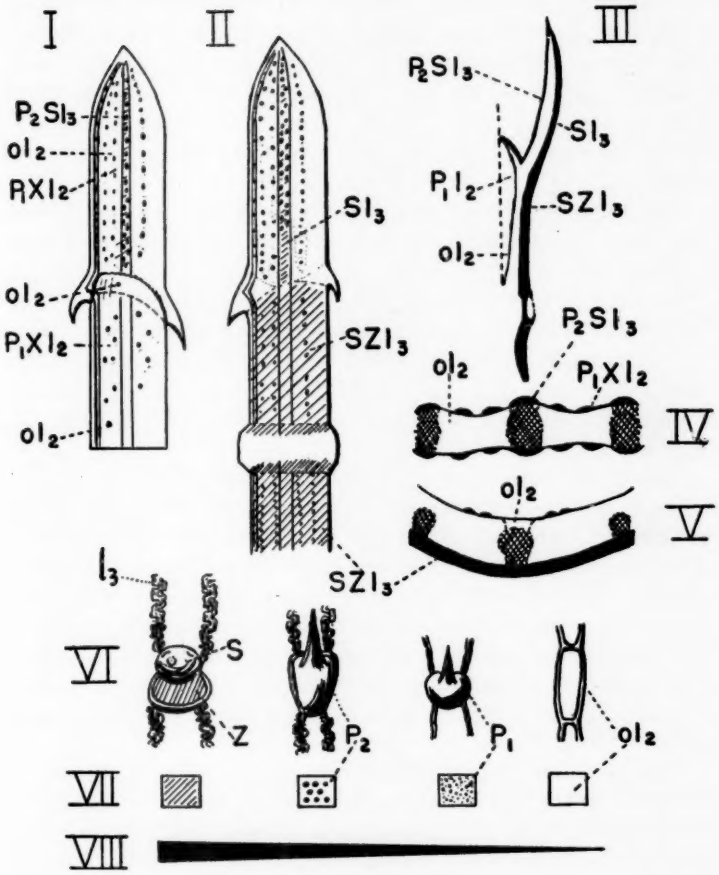


FIG. 15. Examples of dermograms (67). Upper leaf of barley (*Hordeum distichum* L. var. Prinzess). I. Inner face. II. Outer face (only one major vein is figured, with, on the left, an accessory vein). III. Longitudinal section; the thickness of the lines is proportional to the differentiation of the epidermis. IV. Transverse section of the blade. V. Transverse section of the sheath. VI. The principal types of epidermis. VII. Their figuration on dermograms. VIII. Their figuration on sections. S: silica cells; Z: cork cells; P_1, P_2: spicules; X: stomata; l_3: long cells with corrugated walls; l_2: long cells with straight walls; the letter o indicates absence of short cells.

Epidermal Variations in the Consecutive Leaves of a Culm

On the lower leaves of the plant the epidermis is very different from that on the upper leaves. It is almost totally of the homogeneous type (Fig. 16, F_6); only on the veins do some small spicules and silica cells appear. Such an undifferentiated epidermal structure characterizes the "juvenile" leaves in the grass family (67).

Proceeding from the base of the stem upwards, it may be noticed that, from one leaf to the next, there is an expansion of the most differentiated epidermal zones. First of all, the prickles of the veins increase in size and number; the silica cells multiply toward building massive silico-suberous zones which overflow the veins and even cover up the interveinal bands on the outer face of the sheath base (Fig. 16, F_8). In this manner the characteristic arrangement of the upper leaves is progressively built up (Fig. 16, F_{11}; and Fig. 15).

The floral bracts—glumes, lemmas and paleas (Fig. 16, G_1, G_2, G_3)—show the maximum development of this epidermal differentiation. Their outer faces are wholly occupied by the silico-suberous type, and, furthermore, in apical and lateral areas they exhibit a peculiar category of short-pointed exodermic cells (Fig. 17, III, P_o), named "crown-cells" (50, 67). The disposition of the latter elements offers good characteristics useful for identification of genera and species in the tribe Hordeae (67, 96, 161, 162, 191, 200, 238). Awns, when they exist, are armed with strong prickles (P_2).

This gradation in epidermal distribution is a general feature in the grass family, but it may be more or less evident according to the duration of the life cycle of each species. Short-lived herbs, e.g., *Mibora annua* and *Poa annua,* display only a small number of leaves, all of them poorly differentiated. The whole plant thus remains at the infantile stage and can be compared to the neotenic animal species. On the contrary, in xerophilous grasses, such as *Stipa, Elymus* and *Ammophila,* the external face of the upper blades is entirely covered, like that of the sheaths, by a highly differentiated silico-suberous epidermis, reinforced by layers of subepidermal sclerenchyma (200, 202). Cereals, such as barley, our first example, represent an intermediary case between these two extremes.

The gradient of differentiation revealed by these structures is

not only axial but also transversal. We find homogeneous epidermis on the middle of the interveinal band, then, on both sides, exodermic stripes and, finally, silico-suberous epidermis on the vein. Thus each vein offers repetition of the same type of grada-

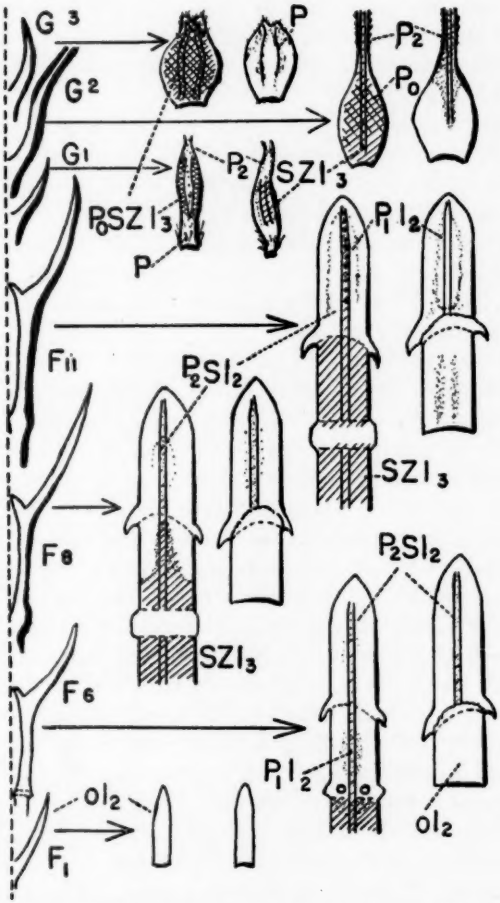


FIG. 16. Histological gradation along a barley culm (67). On the left, longitudinal sections of the leaves and floral bracts. F_1: coleoptile; F_8, F_8, F_{11}: 6th, 8th and 11th leaves; G_1: glume; G_2: lemma; G_3: palea. On the right, dermograms of the same appendages (outer and inner faces). P: hairs; Po: crown cells; other letters are in Fig. 15.

tion observed in the entire culm. A noteworthy feature is that, in furthering this succession, the vein plays a part similar to that played by the apex in the stem. It may be inferred that in both cases the gradient of differentiation is due to a graduated chemical influence, probably a hormone, flowing down from the tip of the stem and unevenly distributed by the veins. Therefore the following sequence can be drawn, notwithstanding the general gradient of senescence, present as usual in every stem and directed downwards (210, Fig. 7):

a) In the culm a multinodal axial gradient appears, shaped as the teeth of a saw with asymmetric slopes, connected with the differentiation of the successive primordia of leaves and nodes and soon indicated in the rosette stage (210, Fig. 10).

b) A uninodal axial gradient, superposed on the preceding one, is directed upwards along the stem, the appendages appearing to be more and more differentiated from the base up (histological gradation of the culm) (Fig. 16).

This disposition seems to be determined by two factors: the apical position of the inductive center of differentiation and the fact that its activity steadily increases during stem development as a result of the quantity or quality of hormones produced. It is well known that each appendage, in the course of its growth, passes through a stage during which its tissues are plastic (210, p. 607). Its final structure depends on the intensity and nature of the hormonal influences which it receives during this period. It is thus easy to understand why the last born of the appendages (adult leaves at the summit of the stem and floral bracts) can reach the highest levels of differentiation, because during their sensitive stage they receive hormones of maximum strength. On the contrary, the older appendages (basal leaves of the culm) are only weakly influenced during their youth by a feeble hormonal activity and remain poorly differentiated. Thus, fixed in an infantile stage, they retain the characteristic structure of " juvenile leaves ".

c) In each leaf the longitudinal gradient is uninodal and directed downwards, the primary distribution center of all substances being the node. In the grass leaf the region which is individualized first is situated at the summit of the organ. This region, the very tip of the leaf, remains poorly differentiated because during its formation it is influenced only by the weak initial flow of hor-

mones. On the other hand the base of the leaf, formed later, is influenced by stronger hormonal action and is extensively differentiated (sheath and base of the lamina, Fig. 15, II).

d) The transverse gradient of differentiation in an adult leaf is multinodal, being bound to the pattern of the veins. On each half of an interveinal stripe it is directed toward the nearest vein which is the place of distribution for hormones as well as for nutrients. It can be noted here that the possible occurrence of a secondary center of distribution for hormones at the tip of the leaf (91) can not modify this concept on the origin of the multinodal transverse gradient. Hormonal and nutritive substances can flow either from the summit or from the base of the leaf; since they are distributed through the veins, they produce the same effect in both cases on the transverse distribution of tissues.

On this basis the histological topography described above in dermograms can be interpreted in the following way. The boundaries between areas occupied by distinct types of epidermis are the materialization of "isopotential lines", i.e., lines along which cell potentialities are bound to unveil in the same way, the cells being placed along them in the same condition during the sensitive stage of their differentiation. Thus along those lines the hormonal and trophic influences are identical—or at least equivalent—in their effect on the cells.

We can regard the silico-suberous and the homogeneous types as representing two fundamental states of equilibrium in the grass epidermis, two stable modes of evolution of the protodermic cell. Between these opposed states we find the intermediate zone occupied by the exodermic type and represented by the slope of the gradients between two levels. This latter region must be considered as a zone of tension between the two basic states of equilibrium in explanation of its extreme variability, contrasting with the uniformity of the preceding ones, and on account of the fact that the isopotential lines are here pressed closely to one another, as are the bathymetric lines on the border of a continent.

Manifestation of Cell Potentialities

We shall not take part in the debate concerning the exact meaning of the term "potentiality" as used by animal embryologists

(93, 115). Driesch (135) uses it to designate those properties segregated in embryo cells at a very early stage of development which appear to be heirs to the "germinal localizations" of the egg. Dalcq (23), on the contrary, is of the opinion that all cells remain for a long time potentially capable of producing all types of tissues and that the destiny of all cells is under the influence of hormonal substances, which he calls "organisines", emanating from specialized centers. These two theses may not be so incompatible as they appear at first, and we think that truth is likely to be found in their synthesis.

Let us apply the term "apparent potentiality" (PA) to those properties of a cell which are actually manifest, and "latent potentiality" (PL) to the properties which are not immediately perceivable but may be revealed in the indefinite future, either in the cell itself—if the latter remains undivided—or in all the daughter-cells which will arise from its divisions. The actual expression of latent potentialities may take place either in normal conditions of ontogenesis or, for some of them, only in exceptional circumstances: variations of environment, wounds, aggression by parasites, etc. In all cases time remains the dominant factor of their revelation.

The sum of apparent properties and latent potentialities constitutes the entire virtual potentiality (PV) of the cell:

$$PV = PA + PL.$$

PV represents the amount of all that a cell is able to give, now and later on, by itself and through its lineage.

Some cells retain the capability of regenerating an entire plant. Their virtual potentiality is then equal to the total of all the potentialities belonging to the species. They are totipotent cells, or cells of maximum potentiality (Pm). Such is the case of reproductive elements, eggs, spores and also of meristematic cells. It can be noted that their apparent potentiality is always weak (pa), while their latent potentiality is considerable (PL):

$$PV = pa + PL = Pm.$$

Other cells very soon display almost all they are capable of, e.g., fibers, cork cells and short epidermal cells. Even in spite of profound changes in their surroundings they remain unchanged. Dedifferentiation in tissue cultures (122) is limited to cells retaining

a juvenile character. For more specialized ones differentiation becomes final (108):

$$PV = PA + pl = Pr < Pm$$

Pr indicates a reduced potentiality, strongly inferior to the maximum Pm, and pl represents the low amount of latent potentiality included in it.

Between those two extremes all sorts of transitions can be observed, materialized by various stages of maturation from a meristem to adult tissues. On a given area around the stem apex or the root tip, the virtual potentiality of the cells remains complete (Pm). In slow growing plants this area may be large, as shown by the interesting experiments of Chouard on Liliaceae (125), in which complete bulbs were shown to form through the proliferation of small groups of epidermal cells on the bulb scales.

But, usually, while PA increases, the virtual potentiality of the cell undergoes conversely a progressive decrease. In the majority of cases the young cell, totipotent when in the meristem, gradually grows into a senile cell whose possibilities are irremediably restricted. It becomes "partipotent" and finally "impotent". It will require long researches to determine the intimate process of this transformation and the factors that influence it (107, 108).

In contrast to this general decrepitude, the steadily totipotent cells, though they are sisters of the preceding ones, escape senescence. This is a fact of paramount importance, to which attention has not yet been sufficiently drawn. It can be traced to the old and so often discussed distinction of Weissmann between Germen (cells of maximum potentiality) and Soma (cells of reduced potentiality). In a plant, however, the Germen includes large numbers of vegetative as well as sexual cells, scattered all over the plant body. Therefore, the distinction between somatic and germinal cells is far less apparent in plants than in higher animals. Instead of proceeding from a sharp segregation at the earliest stages of egg segmentation, the distinction in plants is characterized by progressive instalment of senescence gradients through the mass of meristematic tissues (210, Fig. 7). Between plants and lower animals the difference is smaller: can not for instance, the stolons of polyps or ascidians be considered as belonging to the Germen rather than to the Soma? In short, the evolution of tissues from a meristem can be symbolized as follows:

$$PV = pa + PL = Pm \begin{cases} \nearrow PA + pl = Pr < Pm: \text{partipotent cells} \\ \searrow pa + PL = Pm: \text{totipotent cells} \end{cases}$$

Every cell is derived from totipotent cells. But in certain cell lineages totipotence is transitory ($PV \rightarrow Pr$); in others it is persistent ($PV = Pm$ steadily).

The grass epidermis clearly shows the segregation process of several potentialities during differentiation of a single tissue:

a) cuticular potentiality (formation of a cuticule), generally manifested by all epidermal cells;

b) chlorophyllian potentiality (formation of chlorophyll), appearing in stomatic guard cells only;

c) radial division potentiality, characteristic also of stomatic cells;

d) suberous potentiality manifested only in cork cells (Z), in guard cells (on the ostiole edges) and in tiny spots of some long and corrugated cells (l_3);

e) siliceous potentiality, apparent in silica cells (S) and on the tip of big prickles (P_2);

f) sclerous potentiality, in exodermic cells (P_1, P_2, P_o, P) and in some long cells (l_3), including walls hardening comparable to lignification but with different chemical characters (67);

g) potentiality of wall elongation, on longitudinal faces of long cells or localized on limited areas of the outer face in exodermic and papilla cells;

h) potentiality of transverse division, soon lost by long cells but retained more lastingly by some short cells, e.g., mother cells of subero-siliceous or subero-exodermic couples (Fig. 17, III).

In the initial cells of the epidermis it is obvious that all the foregoing potentialities are present together in a latent state. Never will they be apparent, however, all together in a single cell. Transformation of the huge primitive system of latent potentialities (piled up in a cell) in the secondary system of apparent properties (segregated in diverse cellular bodies), seems to be bound to some definite laws:

a) Some potentialities seem to be antagonistic at the apparent stage. For instance, the suberous and siliceous potentialities are never manifested in the same cell. For their manifestation it seems

to be necessary that the young mother cell (which possesses both in a latent form) be previously divided into two daughter-cells, destined to evolve in two contrasting directions. This segregation is strictly polarized; subsequent development is siliceous in the apical and suberous in the basal cell (Fig. 17, III, SZ) [3].

b) Other potentialities always reveal themselves in the same cell, either successively or simultaneously. For instance the chlorophyllian potentiality is expressed only in those cells which possess the potentiality of radial division, i.e., the stomatic guard cells.

c) Finally some potentialities can appear either in the same cell or in different cells. For instance, the siliceous and sclerous potentialities can manifest themselves together, as in big prickles (P_2), or separately in segregated cells.

The succession observed in this process of unveiling cell potentialities can account for the remarkable mechanism of growth peculiar to the culm of grasses (70, 210, p. 631). A real coaptation exists between the processes of elongation and those of maturation of tissues; in other words, the stages of manifestation of potentialities concerning cell division and modification of cell walls are perfectly coordinated along the scale of time. Such synchronization is governed by apical hormones, every variation in their quantity or activity being able to influence all those manifestations at the same time.

Gautheret has shown that plant tissues cultivated in vitro elaborate their specialized products—chlorophyll, tannin, starch or anthocyanin—only when their mitoses have stopped (150, 151). As long as their proliferation is rapid their chemical activity is turned only to the elaboration of living matter. Likewise epidermal cells are able to reveal their most specific potentialities only when their divisions come to an end.

Another case of interaction between cell activity and nutrient conditions can be found in the interesting observations of Goodwin and Stepka on the rate of elongation of roots (154). On *Phleum pratense* (Fig. 17, I) they noticed that the meristematic zone may be divided in two parts: "the apical 200–300 μ, characterized by

[3] In bicellular hairs (Fig. 17, III, B) a polarized segregation of potentialities can also be observed, the walls of the apical cell remaining thin and soft while the basal cell acquires stronger and harder walls (67).

slow growth and the presence of typical (small, richly protoplasmic, non-vacuolated) meristematic cells; and the basal 125 μ, characterized by extremely rapid elongation and cell division and the presence of vacuolating dividing cells". This interpretation differs notably from the classical conception (228; 210, Fig. 8) by reporting the zone of maximum mitotic activity farther from the apex than is usually admitted, and also by showing a coincidence between the zones of maximum rates in cell division and cell elongation (Fig. 17, Curves C and A). Goodwin and Stepka think that "growth processes in the apical portion of the meristem are probably limited by shortage of food supplies", and they explain this by the following (154, p. 44): "Even though organic materials may be transported by the matured sieve tubes of the protophloem to within 230 μ of the root apex, from there on they must pass through a series of undifferentiated cells which are actively utilizing such materials for their various activities. Hence, a decreasing concentration gradient will be set up, with the most acute shortage at the root apex. Priestley (76) considers this to be the probable explanation for the relatively slow growth and large size of apical cells in the meristems of many vascular cryptogams".

Further on, Goodwin and Stepka express the opinion that "the phrases 'zone of differentiation' and 'zone of maturation' should be avoided, except where a particular cell type is designated. Sieve tubes, for example, are matured well in advance of xylary elements" (Fig. 17, I, p, and x). The maximum activity of cell division and cell elongation coincides precisely with the level where these young phloem tubes begin to appear, conveying an abundant supply or organic materials (Fig. 17, I, F). On the other hand, xylary elements "are probably matured near the point where root hairs commence to develop (Fig. 17, I, H), and when the root becomes prepared to play its absorptive role. Root hairs normally develop behind the zone of cell elongation; otherwise they would be sheared off as the growing portion of the root slid past the soil particles". These observations of Goodwin and Stepka show that root organogenesis requires just as perfect a synchronization as does the development of aerial parts of the plant (210, Fig. 11).

Coming back to the epidermis, we find other examples of coordination in cell-differentiation. The observations of Porterfield

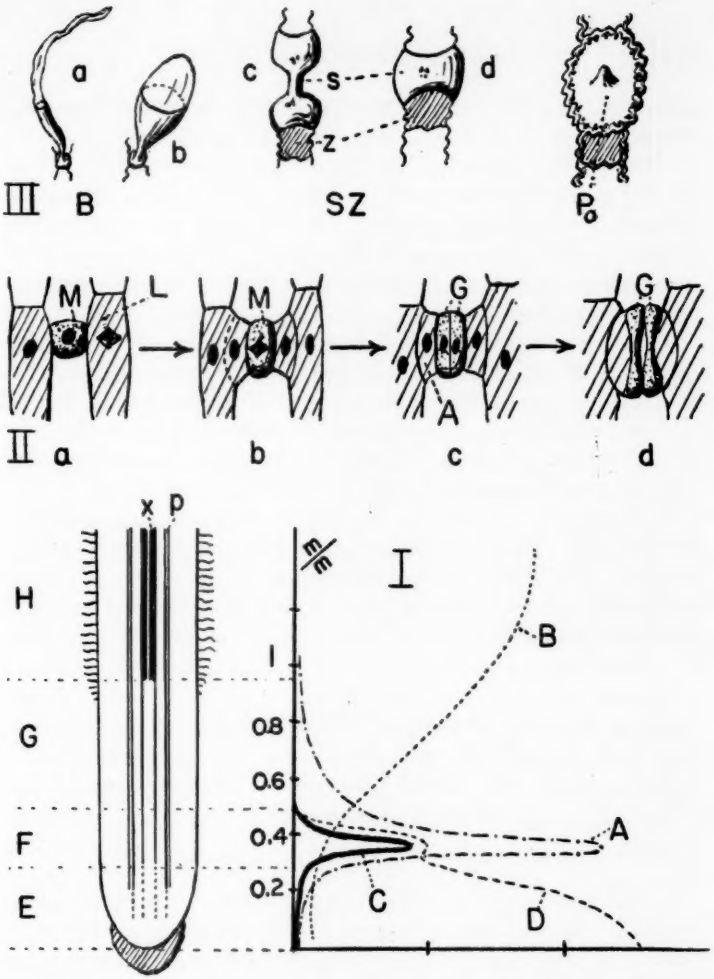


FIG. 17. I. Growth of root cells in *Phleum pratense* (154). The diameter of the root figured on the left is exaggerated to be clearer. A: rate of elongation of the root; B: average length of epidermal cells; C: rate of formation of new transverse walls; D: percentage of wall area laid down as transverse walls; x: xylem; p: phloem; H: zone with root hairs; G: zone of decreasing elongation; F: zone of maximum rates of cell division and cell elongation; E: zone of slow growing meristematic cells.

II and III. Examples of transition between intra-cellular and histological gradients. II. a, b, c, d: successive stages of the differentiation of a stoma in bamboo (65a). The mother cell (M) and the guard cells (G) produced by its division are dotted; the adjacent long cells (L) and the accessory cells (A) of the stoma, produced by their unequal partition, are hatched.

III. Differentiated elements in the epidermis of grasses. B: bicellular hairs: a) panicoïd type; b) chloridoïd type (200). SZ: silico-suberous couples: c) panicoïd type; d) chloridoïd type (67); P_o: crown cell (Hordeae type) (50-67).

(65*a*) on the genesis of stomata in bamboos point out how some interactions may occur between cells of adjacent strips in the course of differentiation. The long cells (L) on the right and on the left of the stomatic mother cell (Fig. 17, II, M), undergo an unequal division which produces the accessory cells (A) of the stoma (quadricellular as usual in grasses). Such a contact reaction between neighboring cells recalls phenomena in the conjugation of many fungi.

This mechanism is deeply influenced in some cases by the nature of neighboring tissues. Stomata, for instance, are produced in epidermal areas superposed on masses of chlorenchyma. It may also be partially controlled by mechanical actions, as on the margins of interveinal strips subjected to mechanical tensions by the unequal growth rates of veins and interveins.

In short, we can discern two principal patterns of epidermal development. In one case the protodermal cell retains all potentialities during a long time and produces the homogeneous type of epidermis. In the other case this cell undergoes unequal partition, producing a specialized element (short cell), capable of giving rise to several more specialized cellular bodies (siliceous, suberous, exodermic cells), and a non-specialized cell (long cell), longer retaining the ability to elongate. This manifestation of local gradients, first intracellular, then involving small groups of cells, is dependent upon the general gradients of the organ, manifesting themselves as anatomical gradations.

CHAPTER VI. ANATOMICAL GRADATIONS

A stem always displays repetition of anatomical units, all fundamentally equivalent but varying in destiny according to their positions (74, 98, 172, 210, 213). Each such unit is a node consisting of a portion of the stem and certain appendages (leaf or scale, axillary bud, adventitious roots).

Grasses

The grass family provides good examples of anatomical gradation. A node at the base of a culm is notably different from a node at the summit. The former is flat and broad; it produces a ring of roots and a strong bud giving an accessory culm or a stolon; its leaf remains short. A summit node, on the contrary, is slender,

elongated and narrow; it is deprived of roots and of lateral buds; its leaf is well developed and, in many tribes, provided with a false node, a cylindrical enlargement at the base of the sheath (50). To these two categories it is possible to add a stolonial type of node on the underground runners (with the appendages reduced to scales), and also a floral type, represented by levels of dissociation of the axis inside the spike or the panicle (137). This diversification of nodal types is due to hormonal influences during the course of development of the stem. Gautheret observed that diminishing doses of hetero-auxins provoke the following effects on tissue cultures of endive (150, 151): isodiametric growth of cells, rhizogenesis (for a concentration of 10^{-5}), cambiogenesis (10^{-6}), leaf elongation (10^{-7}), stem elongation (10^{-8}). This succession recalls both the stratification of levels inside a single node of grass and also the gradation in the structure of nodes along the stem. A multinodal gradient of hormones, with local maxima of concentration at the base of each node, might explain in part both facts. To this influence we must add the local cell reactivity which depends on the local stage of development, thus on the "gradient of senescence" (210), also multinodal in grasses.

Pines

On a pine twig the nodes, small and numerous, are disposed in helices: *a*) at the base of the annual shoot the bud does not develop (Fig. 18, I and II, O); *b*) at a higher level on a male shoot it gives a staminate cone (Fig. 18, I and II, M); *c*) higher up it becomes a short shoot (D) (brachyblast) bearing two, three or five needles, according to the species; *d*) near the summit of female twigs some buds become ovulate cones (F); *e*) finally on all twigs some of the terminal buds remain in a quiescent stage (L), waiting to give long shoots (auxiblasts) the next spring (149, 201).

In all these cases the axillary appendage (euphylle—149) of the node is dwarfed to a brown scale (shown in black, Fig. 18, I). On young seedlings and regenerated twigs, however, this appendage develops into juvenile leaves (Fig. 18, I and II, J) which are thus inserted separately and very different in structure from the adult leaves born by brachyblasts (D) (149).

The succession—sterile buds, male cones, short shoots with adult leaves, female cones, buds of future long shoots—constitutes a

morphogenetic cycle (201). In it, normally, male and female cones exclude each other, except for rare hermaphroditic shoots (Fig. 18, II, M F). They can also be missing simultaneously on young trees, all twigs remaining sterile (Fig. 18, II, ST, and III, St).

In some species (e.g., *P. maritima* = *P. pinaster*, *P. silvestris*) all twigs present only one morphogenetic cycle, but on other pines (e.g., *P. Banksiana*, *P. halepensis*) strong female twigs can display two or three morphogenetic cycles, superposed on one another on a single annual shoot (Fig. 18, II, F P). This structure is said to be "multinodal", in opposition to the preceding one, called "uninodal". The latter expression, though currently used, is inaccurate; being applied to twigs actually possessing a great number of nodes, it refers only to the presence of one single verticil of long shoots, considered here as a sort of "node" of a superior category.

The composition of the morphogenetic cycle could be interpreted, at first sight, as a result of seasonal modifications in growth activity of the twig, the shoot being supposed to produce different types of elements at the beginning and at the end of its annual cycle. Such an interpretation could be admitted if all pines belonged to the "uninodal" type. But the existence of multinodal twigs is sufficient to eliminate this point of view because in this case a shoot displays an ability to complete two or three full morphogenetic cycles during the course of one single annual growth (201).

The necessary conclusion is that the morphogenetic cycle is bound only to the internal equilibrium of the plant, i.e., to its physiological gradients. It constitutes an autonomous mechanism, differentiated inside the bud exactly as is the multinodal structure of a grass shoot in the rosette stage, external factors intervening only afterwards to regulate its elongation. The period of active vegetation can allow the development of one or several of these cycles, according to the species and to the vigor of the shoot. This observation is in full accord with all we have noted on the respective roles of internal and external factors in organogenesis, the former ruling the entire arrangement of the gradient system, the latter only the range of its expansion.

Here again, as in grasses, sexual elements play a large role in the shaping of the gradient system. The flower buds (M or F) evolve more quickly than purely vegetative ones (D or L), and we

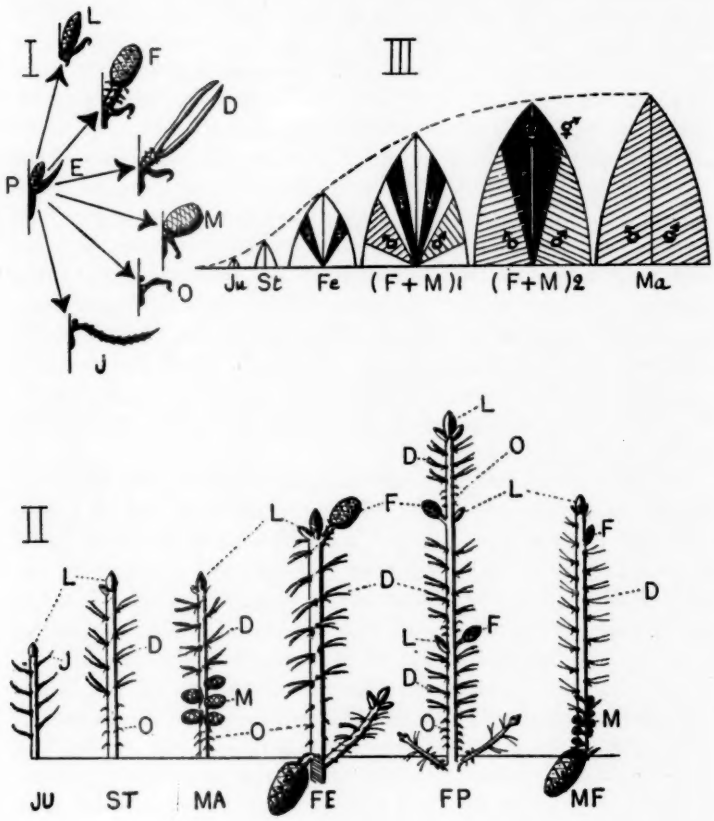


FIG. 18. Anatomical gradations in pine trees (201).

I. Possible destinies of a vegetative point (P) and of its axillary bract (E) (the latter figured in solid black). J: juvenile leaf; O: sterile scale; M: staminate cone; D: short twig with needles; F: ovulate cone; L: bud of long shoot.

II. Schemes of annual shoots. JU: juvenile; ST: sterile; MA: male; FE: female uninodal twig (*P. maritima*); FP female multinodal twig (*P. Banksiana*); MF: hermaphroditic shoot (*P. contorta*).

III. Repartition of sexuality on pine at successive stages. Ju, St: young sterile trees; Fe: female stage; (F + M): the two sexes are developed (adult in full growth); Ma: senile male stage.

can distinguish the following phases (Fig. 18, III): *a*) the young pine is sterile (Ju and St); *b*) in older individuals (Fe) female cones appear near the summit of strong branches but not on the main axis of the tree; *c*) afterwards male cones appear at the bases of small twigs (F + M) 1; *d*) later on, male cones develop abundantly at the base of all secondary branches (F + M) 2, at which time female cones appear upwards, even on the main axis of the tree (during this phase some hermaphrodite twigs can be found sometimes on medium sized branches); *e*) finally the old tree may become purely male (Ma). This segregation of sexes in place and time seems to be in relation to the growth vigor of the branches and also to their tropisms, female sexuality being associated with vigorous and almost orthotropic shoots, male sexuality with weak and plagiotropic ones. It may be noted also that this repartition is similar on the entire tree and on a single branch, female sexuality appearing in both cases in the apical and the male in the basal positions.

Observations on tropisms and on growth of buds give other examples of graded reactions. When the terminal bud of a pine (Fig. 20, I, A) is sectioned (X), a strong orthotropic shoot (LX) is produced by a lateral auxiblast bud (B) and replaces the destroyed axis of the tree. When all the long shoot buds (A, B) of the terminal group are cut off (Y), the normally dormant central bud (C) of a brachyblast located immediately below the section is activated, giving a long twig of juvenile structure (JY), i.e., similar to a seedling shoot with isolated leaves instead of paired needles (101, 198). At the same time, when they have not yet reached their adult size, the needles (D) of the activated brachyblast are stopped in their growth and remain shorter than normal ones. The succession of dominances can be represented thus by:

A/B/C/D/E

In this series (Fig. 20, I) each element (bud or appendage) inhibits the following one; if the former is sectioned, growth of the latter is promoted. These observations reveal a new type of action exerted by one meristematic area on another: inhibition. The inverse type, stimulation, has been described in the influence exerted by the ear of a grass on the growth of the meristematic bases of internodes (210, p. 638). Comparison between these two modes of hormonal influences on meristems will explain the shaping of

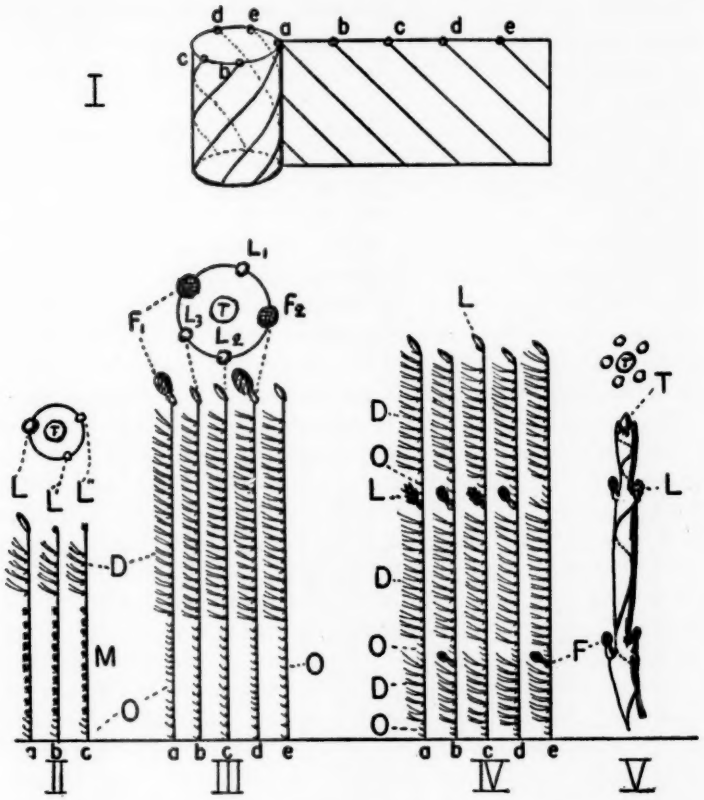


FIG. 19. Phyllotaxic helices in pines. I. Development of five helices (201) (the case of a strong shoot, such as III). II. The three helices of a weak twig, figured as straight lines (letters as in Fig. 18). T: terminal bud. III. Same representation for the five helices of a strong (female) uninodal shoot, such as Fig. 18, FE. IV. Same representation for a female multinodal shoot of *Pinus Banksiana*, such as Fig. 18, FP. V. One single helix figured on shoot IV.

growth gradients. When the propagation of inhibitory actions is at a lower speed than that of stimulation, a multinodal gradient appears; stimulation then induces secondary zones of growth, as occurs in grass culms and in other stems provided with intercalary growth. In the opposite case, growth gradients are uninodal, dominance being exerted at each point more strongly than stimula-

tion, thus preventing establishment of autonomous growth zones along the main axis. Then the growth activity migrates on a set of secondary axes, distributed on the stem according to precise laws.

For the purpose of elucidating these laws, pines are good material. Their buds are distributed on the stem along multiple helices (74, 201), as pointed out long ago by Bonnet (110) and A. P. de Candolle (123). This disposition, however, was afterwards ignored by Schimper, Braun and Bravais (119) who preferred to consider only a single phyllotaxic helix. But recently Plantefol has again drawn the attention of anatomists to the importance of considering multiple helices instead of a single one in phyllotaxic studies (196), and he extended this consideration to all plant families. On pines we can distinguish, for instance, three helices on weak shoots, five on strong ones (201), and the anatomical gradation is well displayed on each helix. Fig. 19 shows in I and III the development of the five helices on a "uninodal" female branch. At the upper end of the annual shoot each helix is crowned by a bud belonging to the types L or F. The ring constituted by those buds gives the apical pseudo-verticil of the shoot. In this example, on each helix the nine or ten nodal points at the base of the annual shoot give only sterile scales (O), while the 20 or 21 following ones give brachyblasts (D) with paired needles.

On a weaker branch (Fig. 19, II) only three helices can be discerned; one is crowned by a normal bud (L), the two others only by dormant buds (L′ and L″). In this example nine or ten nodal points in the middle region of each helix evolve to give staminal cones (M), the three or four basal nodes giving only sterile scales (O) and the five apical nodes paired needles (D).

In Fig. 19, IV, the five helices of a multinodal twig of *Pinus banksiana* are developed; the succession in helix b is:

2 O, 6 D, 1 F, 2 O, 13 D, 1 F, 3 O, 11 D, 1 L.

On a short twig (D) (brachyblast) a helicoidal distribution of the scales surrounding the base of the needles can also be recognized. On *Pinus maritima,* where the needles are grouped in pairs, the scales are distributed in two helices (Fig. 20, II), the needles being for instance the seventh appendage of each helix (A_7 and B_7). The scales possess thin margins extending so widely as to overlap one another on the opposite side of the twig. Coalescence

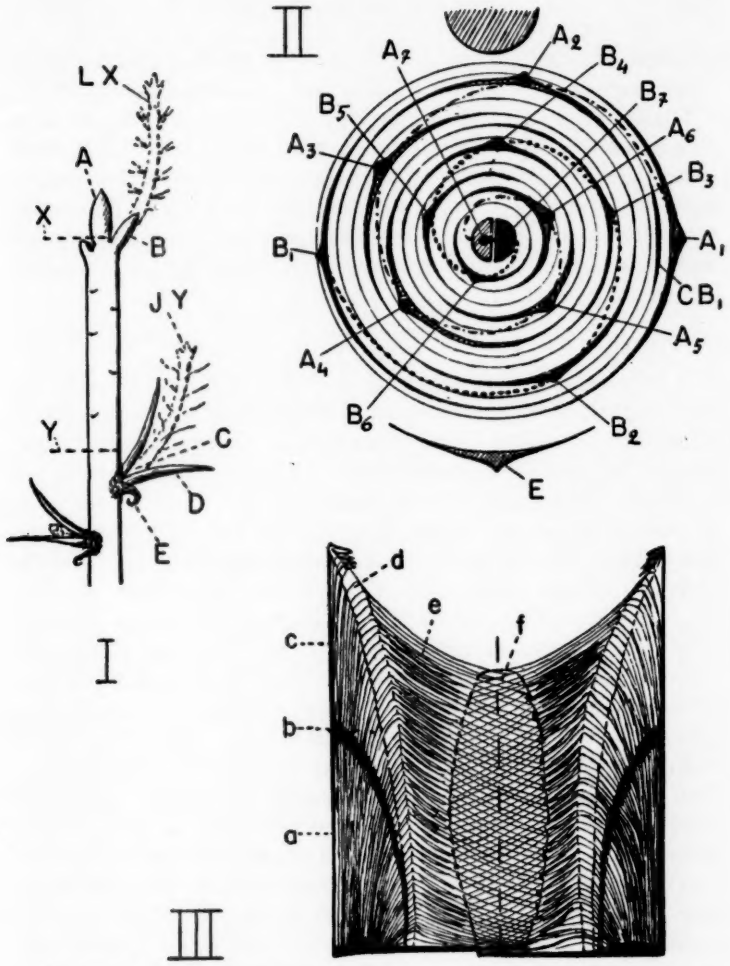


FIG. 20. I. Respective order of dominance of the buds and appendages on a pine twig. X, Y: section levels.

II. Phyllotaxic diagram of a short twig of *Pinus maritima* (*P. pinaster*), showing the disposition of scales on two helices (A and B). CB_1: counterscale of the scale B_1.

III. A scale of short twig of *P. maritima*, longitudinally sectioned on its dorsal median line and stretched out (198). a: chlorophyllian (dorsal) zone; b: anthocyanic zone; c: parched zone; d: margin of the solid scale; e: fenestrated zone; f: counterscale (formed by the ventral coalescence of the two edges of the scale). The curved lines show the direction of lengthening of the epidermic cells. Total length of the scale: 9 millimeters. Isopotential lines dotted.

of these margins accounts (198) for the peculiar organ named "counter-scale" by Bargues (101) and represented in Fig. 20 II, CB, and III, f. The dorsal part (a b c d) of the scale is joined to this counter scale (f) by a laciniate area (e) named "fenestrated membrane" by Bargues. Its slashing is due to mechanical strains exerted during shoot growth on this weakest zone. This scale structure displays a neat histological gradation with isopotential lines, one of them marked by a stripe (b) colored purple by anthocyanin (Fig. 20, III).

Potatoes

Potato sprouts were examined in Part I of this study with respect to their physico-chemical, physiological and auxetic gradients (210, pp. 613–628). They also display anatomical gradations (184). Plantefol has pointed out that, in general, their nodal points are distributed on three helices (196). Such is the case of strong shoots and tubers (Fig. 21, II and III), weak ones possessing only two helices. Basal eyes on each helix give stolons and adventitious roots, while their axillary appendages are reduced to scales (Fig. 21, IV, Y, and V, S). Higher up the eyes give erect branches or remain dormant, and their appendages are fully developed in the form of leaves (Fig. 21, IV, X, and V, F). Thus two parts are differentiated in the stem: the stologenetic region (Y) and the phyllogenetic region (X). The first one is characterized by active root formation; the second by shoot formation. Chemically the former is characterized equally by strong production of anthocyanin in the epidermis and of starch in the parenchyma, while the latter is always the most active for production of chlorophyll. From the histological point of view, the stologenetic area is characterized by formation of protruding stomatic papillae (134). This anatomical gradation in potato sprouts can be compared, with respect to hormone concentration, to the aforesaid succession of zones of activity in grass culms and tissue cultures.

It is well known that the more or less accentuated tendency of certain plants to form stolons is an important taxonomic character, serving as a basis for separation of species or groups of species, as in the genera *Agropyrum* (67), *Cyperus* (142) and *Eriophorum*. Varieties of potatoes also exhibit unequal leaning

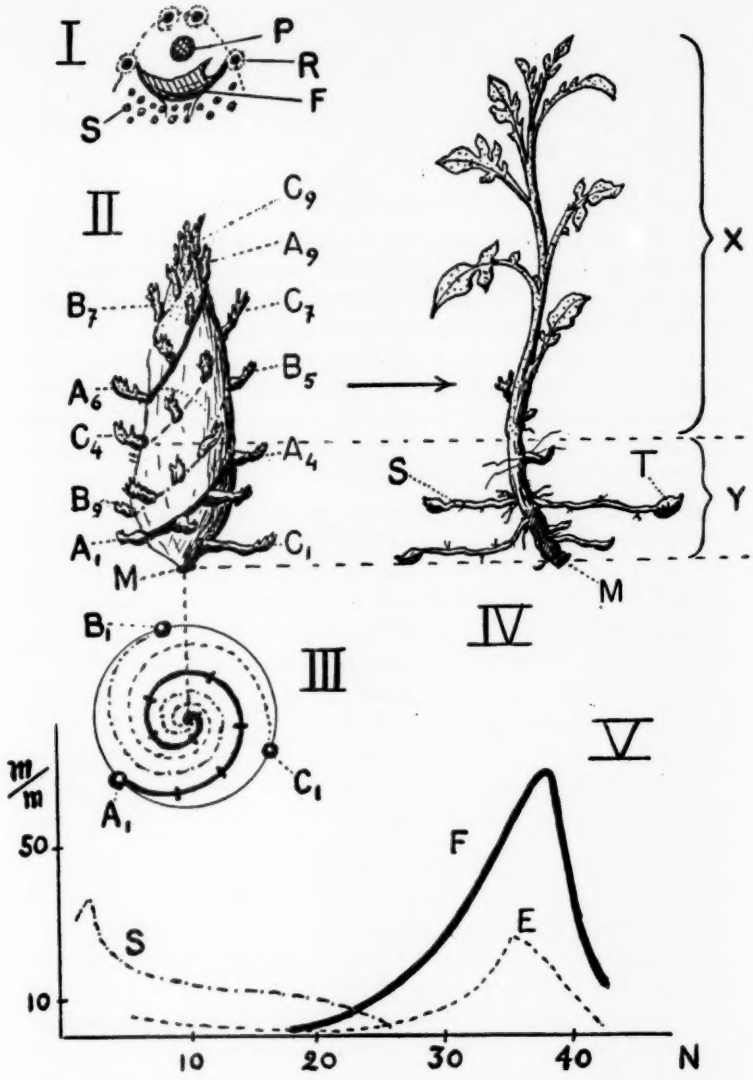


FIG. 21. Anatomical gradation in potato sprouts (74).

I. Scheme of a nodal system. P: bud; R: roots; F: appendage (leaf or scale), S: stomatic papillae.

II. Offshoot showing three phyllotaxic helices.

III. Scheme of the same helices in upper view.

IV. Young potato stem. M: point of attachment on the mother tuber; S: stolon; T: young tuber; hatched: purple area; dotted: green area; X: region of phyllogenesis; Y: region of stologenesis.

V. F: length of the leaves; E: length of the internodes; S: length of the stolons. Numbers in abscissae (N) indicate the rank of corresponding nodes.

toward stolon production, hence notable differences in their agronomic utilization (134).

Sexual Gradients in Cryptogams

While every plant family shows anatomical gradations of some sort (98), reference will be made here only to sexual gradients in some cryptogams. On the strobilus of *Selaginella,* microsporangia are located at the summit, megasporangia at the base. In other words the male organs of the sporophyte appear in an apical position, i.e., the gradient of male sexuality is centripetal. It is exactly the reverse in a phanerogam hermaphroditic flower, where carpels are central and stamens distributed at the periphery, showing a centrifugal gradient of male sexuality [4].

Sex gradients can be observed also in gametophytes. On a *Lycopodium* prothallium, antheridia occupy the central area, surrounded by archegonia. On the contrary, on a fern prothallium, antheridia are in general located at the periphery. Thus in the gametophytes of vascular cryptogams, gradients of male sexuality can be either centripetal or centrifugal, according to the species.

In fungi modifications in growth and sex gradients occur when two thalli are placed together in the same culture. If the thalli belong to different sexes, they induce in each other morphological transformations leading to the production of sexual organs. This mechanism was studied by Blakeslee and Burgeff on dioïcal Saprolegniae, e.g., *Achlya ambisexualis* (104, 121, 124, 222). It appears to be of hormonal nature, female hormones in one thallus inducing the formation of male filaments in the other. Reciprocally hormones emitted by the latter induce the formation of filaments producing oogonia on the female thallus. Definite chemotropisms then appear in the curvature of the threads and result in their final meeting and copulation. These hormonal interactions and their influence to modify growth and sex gradients can be compared to endocrinal correlations within an animal body, but here they are performed through the surrounding space.

[4] If the whole of an inflorescence is considered, centripetal gradients of male sexuality can be detected also in phanerogams: male flowers occupy the axis summit in *Arum,* Indian corn, sedges, etc.; in many Compositae female flowers are located at the periphery of the capitulum, while hermaphroditic ones occupy the center.

Processes of Plant Organogenesis

In short, the following conceptions can be drawn:

a) Initiation of the nodal points. In a growing stem tiny groups of cells, arising from the apical initial mass, remain insulated amidst the differentiating tissues. They retain their juvenile and totipotent character instead of obeying the general gradients of senescence as do the other cells. These tiny groups constitute the secondary vegetative points (nodal points). They are distributed on the surface of the stem according to definite geometric laws, along one or several helices. The number of those helices is determined by the number of radial subdivisions appearing in the apical meristematic mass; it depends both on the plant species and on the strength of the shoot.

b) Elaboration of the nodal system. Each nodal point acts as an organization center. In the middle of it a bud is elaborated, surrounded by: i) an appendage (leaf, scale or bract) sheltering the bud in its axil and inserted on the stem along a crescent-shaped area; ii) a crown of roots (eventually); iii) a vascular system adapted to the needs of the whole and displaying nodifugal differentiation, as shown by F. Pellissier (194). Between these various elements, constituting the nodal system, an equilibrium is established. Frequently the growth of the appendage is antagonistic to the growth of the roots or of the bud.

c) Organization of the bud. At first the gradients of the young bud are uninodal, but soon, in its meristematic mass, tertiary nodal points are initiated (111). This process can be called the organization of the bud. Usually the new nodal points remain small and are distributed on phyllotaxic helices. But in stems with intercalary growth, such as grass culms, the fact is exaggerated to the point of producing undifferentiated levels separating the differentiated ones and extending the multinodal structure to axial gradients themselves. This process, especially conspicuous in the "rosette" stage, can be attributed to the establishment of types of stationary waves[5] in the physiological and chemical system of gradients inside the young tissues (109). It can be compared to numerous features of animal embryogeny, such as strobilization in

[5] This structure may be due, as aforesaid, to the antagonism between opposite tendencies, activations and inhibitions exerted by meristem foci and propagated with different speeds and strengths through the young tissues.

the scyphystom larvae of jellyfishes, differentiation of segments in the caudal part of a worm or metamerism of somites in Arthropods and Chordata embryos (92).

d) Activation. After a stage of rest, of variable length according to the season and also to the hormonal interactions inside the plant, the bud is activated. Its tiny axis, until now hidden between the scales, rapidly increases in length; the internodes elongate and the multinodal structure becomes apparent in the shaping of the shoot.

e) Sexualization. The twig thus produced can remain sterile, but frequently several of its nodal points are affected by sexuality and transformed into simple or compound blossoms. This fact induces extensive modifications in the physiological and auxetic gradients of the stem, which evolves into a more or less complex inflorescence. Usually the sexualized buds display a more rapid growth than do the vegetative homologous elements.

Thus can be conceived the dynamic equilibrium between the internal factors which concur to build the gradient system and to shape the plant body. It is modified by many external factors of physical, chemical and biotic natures.

CHAPTER VII. MODIFICATION OF HISTO-PHYSIOLOGICAL GRADIENTS

Action of External Factors on the Gradient System

A gradient is never modified alone. Whenever external factors intervene, all gradients are transformed without any rupture of their mutual interdependence. In other words, the system is distorted as a block instead of being thoroughly upset.

Modifications produced in plant structure by variations of the environment have been frequently investigated. There have been studies on the influence of submersion on the development of stomata, and of light on the structure of leaves, stems and roots (129, 130, 142, 182). Bonnier has obtained marked condensation in the gradients of elongation by transferring plants, e.g., *Helianthus*, from lowland stations to high altitude experimental gardens (112). Mlle. Larbaud has shown that the resulting modifications are in the vegetative parts and not in the structure of the flower. The number of blossoms and the length of peduncles are reduced by the altitude, with the result that the inflorescences become smaller and more compact (167). At its upper altitudinal limit each

species tends to become uniflorous, while its vegetative body becomes drastically reduced both in the length and in the number of its internodes. Flowers are often said to be larger in mountains than on plains, but this is true only by comparison with the height of the plant bearing them. The ratio in size between flower and vegetative apparatus is 15 times greater in *Lotus corniculatus* growing at an altitude of 2,900 meters than in specimens living in flat country, but absolute dimensions of the flower are about the same in both cases (167).

From the histological point of view, Mlle. Larbaud points out that modifications are the more accentuated as the tissues occupy a more external position (167). The epidermis is transformed to a greater degree than the internal tissues, the calices more than the corollas, and the latter more than the reproductive organs. In mountain stations hairs and papillae are more developed, stomata more numerous, nectaries more conspicuous. This fact is related to greater secretion; altitude is known to increase the production of perfumes and essential oils. Anatomically the radial gradients of the stems are also modified; the bark is hypertrophied relative to the central cylinder.

From these observations it may be concluded that altitude deeply modifies the gradients of the vegetative apparatus, but only lightly those inside the flower, the "intra-floral" gradients. The latter always exhibit considerable fixity, while vegetative gradients appear flexible.

Inflorescence responses are shared between these two opposite tendencies: stability, by its floral nature, and variability, by its vegetative properties. When the stem possesses strongly condensed floral gradients, the first tendency becomes dominant. For instance, in the Compositae, Dipsaceae and Plumbaginaceae Mlle. Larbaud observed that each capitulum (head) always bears approximately the same number of flowers at all altitudes. Only the number of capitula is reduced, and at the upper altitudinal limit the plant bears only one of them. Thus the gradients of the capitulum have acquired the same fixity as those of a flower, and it may be considered that in those families the principal floral unit is no longer the flower but the head (167).

The above situation can be compared to that in the grasses, where a spikelet constitutes the real floral unit, within which the

gradients acquire notable fixity. When the plant grows under unfavorable conditions, for instance, on a dry limestone rock, its spikelets remain normally constituted, but their number is reduced, the stem shortened and ultimately the plant may be dwarfed to a tiny culm bearing one single spikelet (199). In dry country, on flat rocks, it is possible to observe entire associations of microphytes belonging to various families—Gramineae, Cruciferae, Saxifragaceae, Compositeae, etc.—each reduced to a dwarf stem one to three centimeters high, bearing one single leaf, of small size, and one single floral unit: spikelet, flower or head as the case may be (199).

Biometric studies on grass culms reveal the progressive fixedness of gradients when drawing nearer the sexual elements. In rice (28, 210, Fig. 14, IV) the gradation observed in the upper part of the culm is very regular for all specimens and varieties, while large fluctuations occur in that of the lower part. Thus the prefloral upper region of the culm, endowed with steady gradients, is opposed once more to the vegetative basal region, the latter showing fluctuating gradients and being more responsive to external influences.

All these examples show the summation of many factors, but the peculiar mode of action of each can be discriminated to a certain extent. Temperature is known to be one of the most powerful agents capable of modifying histo-physiological gradients. Vernalization utilizes this factor in producing useful modifications (157, 163, 175), and in the first part of this work (210, p. 616) gradients of sensitivity of tissues to heat have been examined. Effectiveness of heat in modifying the sex gradients in fungi has been shown by Schöpfer (124, 224) who demonstrated that by varying the temperature it is possible to induce the formation of concentric zones of egg production in Mucorinae cultures, i.e., the appearance of a multinodal radial gradient of sexuality in thalli which otherwise would remain homogeneous (124). M. A. Lessler has noted the effects of gradients of temperature on moisture gradients in plant tissues: when one side of a fruit is heated, water is displaced and concentrates in the cool side (168).

Light also is a powerful factor of modification. Its intensity, its periodicity and the wave length of its component radiations in

various ways transform auxetic and metabolic gradients. As it controls all gradations of photosynthesis, of food stuff migrations (21, 153), of proteosynthesis (193), of auxin repartition (126, 127, 128, 234, 236, 245) and, through them, of elongation (22, 35, 192), light really shapes the gradient system and thus the entire plant body. This factor can produce lasting effects, and Lysenko has shown the possibility of obtaining results similar to vernalization by withholding light at certain stages (163, 175).

Moisture also, as well as temperature and light, exerts influence. It is possible to demonstrate that a seedling must pass through a succession of stages, the hydro-stade (204), the thermo-stade, the photo-stade (175), each of them characterized by a dominant reaction towards one of these fundamental factors. In other words, normal development of the young plant requires, during definite lapses of time, first a particular amount of moisture, then a certain temperature and pressure of oxygen, and finally a suitable intensity of light and amount of carbon dioxide.

The seedling is able to pass from one stage to the next only when the due ration of water, light or heat demanded for the preceding period has been obtained. Maxima and minima can be recognized; when they are transgressed, anomalies are produced in auxetic and sexual gradients. Studies on photoperiodism have shown that too short or too long illumination can suppress flowering or fructification of a plant (127, 128); in other cases dwarf stems are produced.

It would be useless, however, to introduce a factor prior to its turn, for instance, temperature before water or light before temperature, because it would then be ineffective (204). It would be erroneous also to consider each stage simply as the phase during which the seedling is the more sensitive to a given factor. In reality a new stage represents the moment from which onward a new factor becomes effective. A mature and dry seed constitutes a mechanism fit to react first to one single agent: moisture. It is then at the static phase of the hydro-stade. When soaked it enters in the dynamic phase of the same, which is characterized in microcalorimetric studies as "physico-chemical thermogenesis" (205, 206, 207, 208) (Fig. 22, O A B). After a lapse of time (Fig. 22, B C), variable according to species and conditions, the seedling enters the thermo-stade, characterized by the rise of a "biological

thermogenesis" (Fig. 22, C D). The concomitant increase of respiratory intensity explains why, at this stage, a certain amount of oxygen becomes necessary for the plant.

Preliminary dehydration of the seed can introduce modifications in subsequent stages by intensifying the physico-chemical and the biological thermogenesis to occur after soaking (Fig. 22, A' B C D') (206). In general it can be said that the lack of a factor or

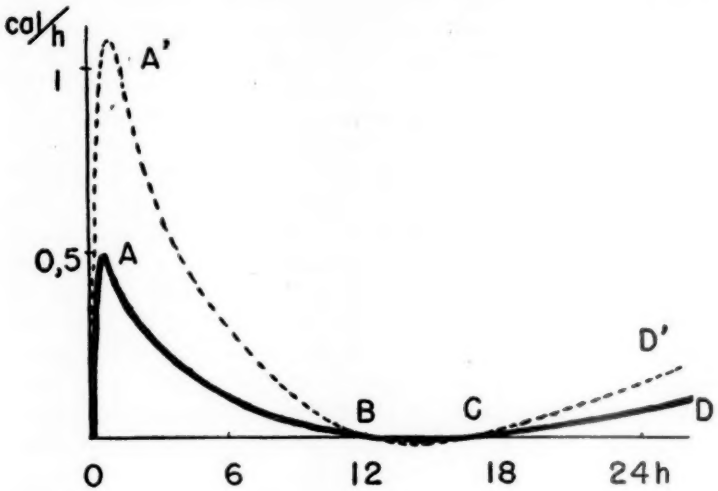


FIG. 22. Thermogenesis in wheat germination (one gram of grains at 17° C). O A B: physico-chemical thermogenesis (soaking of the dry seed); B C: time of rest; C D: biological thermogenesis (increasing rate of respiration). Dotted curve O A' B C D' shows thermogenesis of grains previously dehydrated during three days. In abscissae the times in hours; in ordinates the thermic flux (rate of heat production) in calories per hour (208).

excessive intervention of it at the moment when the seedling begins to be receptive towards it, induces in the seedling a lasting disturbance in its physiological gradients. Dehydration at the static phase of the hydro-stade, cold at the thermo-stade, darkness at the photo-stade, all modify the ultimate growth, as occurs in vernalization (127, 128, 163, 172).

Tropisms. Tropisms can be considered as modifications of auxetic gradients under the influence of external factors. In fact a

tropism should always be interpreted as the expression of a transverse gradient of growth in a place where such a disparity is normally absent. The classical experiment of Went on *Avena* coleoptile was the discovery of the immediate cause of this phenomenon: the birth of a transverse gradient of auxin concentration (91, 113, 114, 223, 241, 242).

But along the parts of a plant the intensity of tropic .esponses is itself subject to gradations. Such gradients of tropisms appear thus to be in reality second order or compound gradients: axial gradients dependent on the intensity of transverse gradients of growth. For instance, the buds at the base of a potato sprout are plagiotropic (Fig. 21), giving horizontal stolons, while apical buds are orthotropic. The same disposition exists in all erect plants:

a) In the main roots there is a maximum of positive geotropism, producing the holding system.

b) In secondary roots there is weaker positive geotropism, changing into plagiotropism at the periphery (102).

c) In the lower branches there is weak negative geotropism, replaced by plagiotropism in decumbent forms.

d) In the main axis of the trunk there is maximum negative geotropism, becoming full orthotropism in erect plants.

This distribution of tropisms is one of the strongest manifestations of the general polarity of the plant and enables it to make full use of its spacial environment; it is connected not only with gradients of hormones but also with all metabolic gradients.

On the other hand, the gradation of tropisms is frequently associated with anatomical gradients. In pines, when the strong orthotropic shoots (201) possess five phyllotaxic helices, the weak plagiotropic ones produce only three (Fig. 19, II and III). On *Hedera helix* Mlle. C. Roche has shown anatomical differences between orthotropic twigs, producing simultaneously two leaf primordia at their apex and subsequently developing two normal helices, and plagiotropic twigs, giving birth to only one leaf primordium at a time and thus to a distichous disposition of leaves (220).

Chemical Agents. Data have been gathered on the influence of chemical agents on plant gradients, chiefly on auxetic ones (155, 173, 174, 187, 212, 217, 218, 227). It is well known, for instance,

that in an acid soil tree growth is slackened (197). H. Olliver has recently studied the action of alkaloids, sulfamides, vitamins, toxic salts, venoms, antibiotics and many other substances on wheat seedlings (190), revealing the existence of gradients of sensitiveness toward toxic agents:

a) Meristems are the most sensitive of all tissues. The more a tissue is differentiated, the more it is resistant. This fact can be compared to the aforesaid observations on the influence of heat (longitudinal gradients of sensitiveness) (136, 210).

b) In a given organ the various tissues show unequal degrees of sensitivity. For example, in a root the resistance increases from the outer part towards the center (radial gradient of sensitiveness).

c) The different organs of a plant are unequally sensitive. Leaves offer the highest resistance, then the stems. Roots are the easiest to injure; a concentration of toxin may be lethal for them while only crippling the leaves and stems (Fig. 23, I, C).

Thus anatomical and histological gradients reappear in this peculiar field of sensitiveness; they are related both to the general polarity of the plant and to the state of maturation of the tissues. Their summation constitutes the toxin-sensitivity gradation of the plant (190). This gradation is about the same for all physical and chemical agents. On the other hand, however, it is widely different from the gradation of sensitiveness to biotic agents (210, p. 617); for instance, meristems, which resist the invasion of many parasitic organisms (fungi, bacteria, etc.), are the most vulnerable tissues to chemical or physical agents. Mechanisms of resistance are radically different in the two cases.

From another point of view toxic agents always provoke extensive disturbance in all physiological and histological gradients of the plant, e.g., in auxetic gradients, gradients of cell-differentiation, metabolic and hydration gradients. The influence in some cases is only negative, resulting in deterioration of the organism. In other cases, minor doses of toxins, called "diphasic" for this reason, stimulate growth or physiological functions, notwithstanding the depression produced by heavy doses (190). Finally some deep modifications of morphology, such as tuberizations (Fig. 23, I, B), can result from disturbances in the gradients of growth and metabolism caused by colchicine, cacodylates, trypaflavin, sulfamides,

etc. Ollivier has distinguished many categories of cytological lesions. Some of them are commonly found in every case: mitoinhibition, pycnosis, alterations in the nuclear shape; others are selective, being present only with specific toxic agents: chromosomal dispersions and aberrations, tropocinesis (rotation of the spindle), nuclear vacuolation, nuclear excretion, etc. Lesions of the first class may be reversible when slight; lesions of the second class are always irreversible and must be considered as "preagonic".

Regarding their mode of action, toxic agents can be divided into "monophasic" ones, producing only inhibitory effects, and "diphasic" ones, producing, as seen above, a stimulating or an inhibitory influence, according to the intensity of their action (190). Among the monophasic fundamental toxins are salts of lead and mercury, saponins, penicillin, tuberculin, some alkaloids (atropin, etc.) and some sulfamides (dichlorosulfamide-benzoate of sodium; 237 M; 402 M; 2255 RP; 2090 RP). Among the diphasic fundamental toxins are vitamins B, C, K, PP; some alkaloids (strychnin, nicotin) and some sulfamides (809; 1162 F; 640 M; 693 MB). Among the diphasic selective toxics are colchicine, trypaflavin, venom of the honey bee and sodium cacodylate.

Other extensive investigations have been made on the effects of colchicine and other substances on cell nuclei (226). Mangenot and Gavaudan, working chiefly on root tips of *Allium*, observed numerous localized and graded anomalies (152, 178): polyploidy (105), fusorial inhibitions, chromosomal contractions, pcynosis, amitosis, nuclear buddings, tropocinesis, changes in the duration of mitotic phases, etc. The importance of such researches lies in their connection with the cancer problem and the influence of carcinogenetic agents (169). From the point of view of our present work, they reveal the mode of appearance of gradients in nuclear structures inside the plant body. This field is at present only feebly explored, but it can acquire huge importance by shedding light on the above mentioned problem of unequal repartition of potentialities among newborn cells (gradients of senescence, etc.).

Numerous experiments have been performed also on the effects of growth substances used in weed control, such as 2,4-D (2,4-dichlorophenoxyacetic acid) (100, 144, 159, 214). Bachofer has observed that naphthylmethylacetate applied in lanolin on bean

plants exerts a weaker influence than 2,4-D, but that this influence is neatly graded (99): epidermis, pericycle, outer cortex do not respond and are exfoliated, while inner tissues display anomalous growth. The central cylinder is deeply affected in all parts, chiefly in its cambium; endodermis is disturbed and can give rise to vascular elements. New roots are induced from medullary rays within one centimeter from the treated surface and on the tumor. It is easy to distinguish here the two above mentioned aspects of the phenomenon: gradient of sensitivity for the toxin and modification of auxetic gradients.

Murray and Whiting have noticed that gradients of sensitiveness are different for diverse salts of 2,4-D: the calcium and magnesium salts induce strong cell proliferation in the peripheral tissues of the bean plant (186). With copper salts the multiplication is limited near the surface but most active at a depth of two or three millimeters; with ammonium salts the region of greatest proliferation is even deeper. Below it the authors noticed a zone of root production, then a zone of decreasing cell division. It may be remarked that both the gradients of sensitivity and the shaping of auxetic gradients can vary with the chemical employed, but that their general pattern remains the same. Stewart and Klotz have obtained similar results by using sprays of 2,4-D on maturing fruits (231). Blossom drop and immature fruit drop are retarded, and fruit shape is transformed, some fruits becoming cylindrical and oranges acquiring strange shapes with excessive navel growth.

Physiological gradients also are disturbed by chemical agents. Heilbrunn, for instance, has noticed variations in gradients of cyclosis (protoplasmic streaming) by changes of carbon dioxide concentration (158). Wanner has shown that addition of glucose can double or treble the respiratory intensity in the active root hair zone, changing the pattern of the entire respiratory gradient of the root (239), while hydrocyanic acid depresses the same intensity. J. H Taylor has investigated the action of many substances on excised anthers and demonstrated that the occurrence of meiosis is governed by the establishment of chemical gradients inside the tissues (232).

Furthermore, the broad field of investigation dealing with experimental transformation of plant gradients is not limited to

chemical substances. Physical agents, such as X-rays, γ-rays and ultra-sounds, have proven effective in the production of nuclear alterations and growth modifications (147, 190). Their effects can be exactly paralleled by those produced by chemicals. Ollivier has shown that X-rays can be classified with the diphasic selective toxins because of their action on wheat seedlings, radium emanation with the monophasic ones (Fig. 22, I, D), and ultra-sounds with the diphasic fundamental toxins (190). This parallel between the effects of physical and chemical agents must certainly indicate similar fundamental modes of action on graded properties of the tissues.

A new means of investigation has recently been acquired with the availability of radio-active isotopes of the atoms used in the building of living matter. They have recently proven valuable as tracers in detecting gradients in the fixation of carbon, nitrogen, phosphorus, iodine, etc., and in measurements of their variations.

Working with P_{32}, Rabideau, Whaley and Heimsch have shown in maize that maximum radio-activity occurs in the more apical internodes, and this earlier in hybrids than in inbreds, a fact associated with quicker development. They have detected also a progression of localized radio-activity from the tip to the base of the leaf (215, 216). Mericle has discovered that the gradient of accumulation of the same radio-active phosphorus P_{32} differs in the leaves of normal and Rg mutant maize. According to this author: "Accumulation pattern differences suggest "potentially ragged" areas *prior to the visible manifestation* of the character" (183). Such results demonstrate what a powerful weapon tracer atoms are in the hands of biologists for investigating all apparent and even unapparent gradients in plant tissues.

Biotic Agents. Biotic agents can provoke the greatest disturbances in physiological and histological gradients. Every contact with a foreign organism induces in the plant body a series of reactions subject to regular gradations and often deviating to a large extent from normal organogenesis. Noel Bernard has shown how fungi produce tuberization in orchids (7). As a response to the parasite intrusion, the host cells change their division and differentiation patterns, giving bulky polystelic tubers instead of slender roots. Deformations produced by rusts on conifer

branches are well known as " witches brooms ". In them physiological as well as auxetic gradients are thoroughly transformed; Maresquelle has shown, for instance, that the respiratory intensity of the contaminated tissues is increased (56, 180, 188). Modifications of growth gradients of *Euphorbia cyparissias* attacked by *Uromyces pisi* and of tree leaves by other rusts (Fig. 23, IV) are commonly observed. Recently Killian has described the distortions produced by *Tuburcinia Schizocaulon* on *Odontites lutea* (165). In this case young tissues exert a real attraction for the hyphae which are thus " cambiotropic ", in contrast to what appears, for instance, in yew tree mycorrhiza, where fungi are " cambiofugal " (66). This acropetal gradient of infestation produces in *Odontites* an hypertrophy of stem apices with partial abortion of flowers; necrotic zones appear, being, of course, a part of the defense mechanisms of the host, as they result in insulation of the parasite.

Nodules produced on the roots of leguminous plants by nitrogen-fixing bacteria are another example of transformation of auxetic gradients by biotic factors. In these nodules cell-division is accelerated, giving masses of tissues where the symbiotic bacteria swarm and where new radial gradients of differentiation appear (Fig. 23, V), including the establishment of an exceptional vascular system (235).

With a totally different result, it is possible to point out some analogies with the action of *Bacterium* (*Agrobacterium*) *tumefaciens* (140, 179, 219, 221). In experimental cancers produced on *Chrysanthemum* by inoculation with this parasite, it is possible to observe nodules surrounded by concentric zones of suberous and vascular differentiation. This fact can be compared to observations of Gautheret, Nobécourt, de Ropp and White, showing in tissue cultures the formation of zones of active proliferation with cells orientated as a cambial layer, while other regions, where proliferation is slackened, produce aberrant xylary elements (150, 151, 189, 221, 243, 244).

In all cases of production of tumors and tubers by biotic action modifications of tissues begin at a conspicuous distance from the cells containing the tuberizing agent. These modifications seem thus to be determined by diffusible substances elaborated either by

the endophyte itself or by the host tissue as a reaction against the invader (116, 117, 118, 120). Furthermore, tuberization appears as a phenomenon endowed with a certain autonomy and capable of being induced by factors of different kinds. It presupposes great modification of all physiological, auxetic and histogenic gradients:

a) Changes can be noted in the orientation of mitoses; instead of being longitudinal, numerous spindles are transverse, hence the occurrence of partitions in all directions, giving a massive shape to the organ. Such rotation of the spindles, which are no longer orientated with respect to the organ axis, may be compared to tropocinesis observed under the influence of toxins (152, 178, 190).

b) Gradients of cell enlargement are also modified; elongation is lessened but, conversely, the cells are hypertrophied in directions perpendicular to the axis, becoming thus iso-diametric. This fact can be paralleled to effects produced by auxins at high concentration (150).

c) Spherical gradient fields (physiological and histological) are initiated in place of cylindrical ones, resulting in a new shaping of organs which become globular instead of elongated.

d) Metabolism is transformed. Anabolism dominates catabolism, resulting in a large accumulation of reserves.

Thus a new organ—a tuber—is initiated, provided with local autonomy and specific patterns of differentiation, escaping more or less from the general regulations of the plant. In some cases it acquires greater longevity than the plant itself, and this observation led Noel Bernard to his general concept tracing the origin of perenniality in plants to symbiosis and tuberization (7). But now it appears that tuber-formation is not necessarily symbiotic, since it can be induced also by simple physical agents or chemical substances (210, 221). Thus the concept of Noel Bernard must be revised as follows: tubers can be fungous galls (myco-cecidia), bacterial galls (bacterio-cecidia), virus galls (viro-cecidia) etc. (103), but they can also be initiated by the internal mechanism of the plant, either spontaneously or in response to outer physico-chemical influences (toxins, radiations, variations of osmotic pressure, addition of sugars, etc.) (126).

Tuberization may be considered an inherent feature of a plant

whenever the tuberized parts present a perfectly regular morphology, always appearing on the same organs in the same places (141). Their histo-physiological gradients then are a part of the regular system of the plant. Such is, in general, the case in bulbs; they present in their shape a perfect regularity, manifested by an immutable disposition of scales (125). In this case it is highly probable that tuberization is a constant property of the plant. Normal hormones play here the role of tuberizing agents; they are emitted at well-defined points, at determined moments, and they are always distributed according to perfectly regular gradients.

A different case is presented when tuberization is induced by an alien organism. The latter can irregularly be present or absent; it can intervene in one place and not in an anatomically similar one; it can be virulent or attenuated, producing strong or weak effects (7). The result is that, in this case, tuberization itself incurs numerous irregularities and variations. This recalls the behavior of dermotropic viruses which do not affect the totality of the diseased skin but localize irregularly in some parts of it, producing pustules or pimples. Examples of this second category are given by symbiosis between orchids and fungi (7).

Wholly apart from these well-classified types, the potato tuber offers one of the most extensively discussed cases by reason of its economic interest and of its peculiar features. On a potato plant tubers are produced on some stolons but not on all; they can appear at the base, on the middle or at the tip of the stolon; they may include a variable number of internodes and their shape can change, even in one pure strain. Furthermore, tubers may be produced on aerial stems, according to variations of the environment (106), or those stems, entirely affected by tuberization, assume cactus-like shapes (195). Finally, when young potato plants are obtained from seed, only some of them tuberize, others remaining slender, non-tuberized and thus useless. This fact has compelled farmers to propagate potatoes only by tubers and not through seeds, notwithstanding the inconveniences attached to the former method.

This variability in the tuberizing process has suggested to many biologists the idea that this process is not a normal feature of the potato plant but a pathological deviation. Such is the opinion of Noel Bernard, Costantin and Magrou, reviving old beliefs of

South American Indians. What may be the tuberizing agent? The above authors have supposed that it is a fungus (131, 176); but in most cases it is impossible to detect any fungi in the tubers. Cuénod has expressed the opinion that the agent may be a form of *Rickettsia,* naming it *R. solanituberosa* (132). It would be the first record of this genus in phytopathology, for *Rickettsia* otherwise is known only as a parasite of animals. However, the question remains open that the tuberizing agent may be related to the infra-bacteria or viruses, many of them being known as intracellular parasites of plants. Perhaps it will be settled in the near future with the help of the electron microscope.

Controversies between supporters of the pathological and those of the physiological interpretations have been partially clarified by recent comparisons between viruses and genes. We could for instance consider in potatoes the existence of a tuberizing factor, and name it " factor T ", regardless of its true nature. The local concentration of this factor would determine in the tissues the following changes in their auxetic and metabolic gradients: *a*) local slackening of elongation; *b*) preponderance of radial cell divisions, resulting in the organ thickening, chiefly with pith hypertrophy; *c*) local accumulation of starch; *d*) permanent growth inhibition of foliar appendages; *e*) temporary inhibition of roots. On a slender stolon this set of transformations produces a tuber; when the factor T reaches erect stems, it results in their producing aerial tubers or twigs displaying anomalous shapes. Mlle. Piettre has shown that such cactus-like potato stems often exhibit teratological malformations of their flowers (195), a fact which may lend support to the hypothesis of factor T being a virus rather than a normal growth substance. Furthermore the frequent sterility of potato flowers could be explained through a remote influence of factor T present in the lower parts of the plant. Manifestations of factor T are subject to external and internal conditions, and tuberization may be the result of many agents, working alone or together. It would explain why some observers have attributed tuberization to fungi, while others observed the same without any detectable alien organism. In the former case the fungus could have acted only as a stimulant, affecting either the virulence of factor T or the reactivity of host cells toward it; in the latter, the activity of factor T would have been aroused by chemical or physical agents.

Galls Produced by Insects and Mites. Among modifications of gradients by biotic agents, insect-made galls deserve special mention, for in them a new factor appears: an intricate combination of reflexes and instincts working through a highly organized nervous system. The result of this intervention is extensive modifications of the gradients fields of the plant. The following types of galls may be recognized according to the three great groups of insects that induce their formation:

a) The most elaborate galls are produced by Hymenoptera, namely Cynipids (Fig. 23, II and III). They are closed cecidia, perfectly insulating the larva from the environment (145, 148, 160, 180, 240). A nutritive tissue is generated inside, in contact with the larva and protected outside by a lignified envelope. Marked hyperplasia and cell hypertrophy occur (166), cell nuclei being themselves hypertrophied with alteration of mitotic processes. In such Hymenoptero-cecidia the maximum transformation of plant tissues is brought about.

b) Galls produced by Hemiptera and Acarina (mites) are simpler (148). They are open, cone-like as those of *Eriophyes,* or consisting of leaf deformations. Histological modifications are weak, there being only slight hypertrophy and hyperplasia with homogenization of parenchyma; mitoses remain normal.

FIG. 23. Modifications of gradients through physical, chemical and biotic actions.

I. Gradient of sensitiveness of wheat seedlings to toxins (190). A: control; B: weak dose of sulfamides; C: strong dose. The root is more sensitive than the leafy shoot: in B the roots are tuberized; in C they are entirely atrophied while the shoot is only curved. D: action of radium emanation (4,000 U.R. in 24 hr.); the roots are atrophied, the shoot only crippled. T: tubers, R: roots. The arrows show the gradients of sensitiveness.

II. Gall of *Andricus sulfureus* Weld. on a leaf of *Quercus arizonica* (Weld and Porter Felt) (145, 240). Arrows point the direction of gradients: normals in the leaf; abnormals and centered on the insect larva in the gall. K: place of the initial group of injured cells acting as origin of the cecidian blastema.

III. Gall of *Amphibolips gainesi* Bass. on an acorn of *Quercus marilandica* Muench. (145).

IV. Hypertrophy of parenchyma on an apple leaf by the influence of a rust fungus (myco-cecidia). Hatchings show the infested region. P: pycnia; Ae: aecia.

V. Hypertrophy of a clover root under the influence of nitrogen-fixing bacteria (bacterio-cecidia). Infested area (Ba) is dotted; conducting elements are hatched.

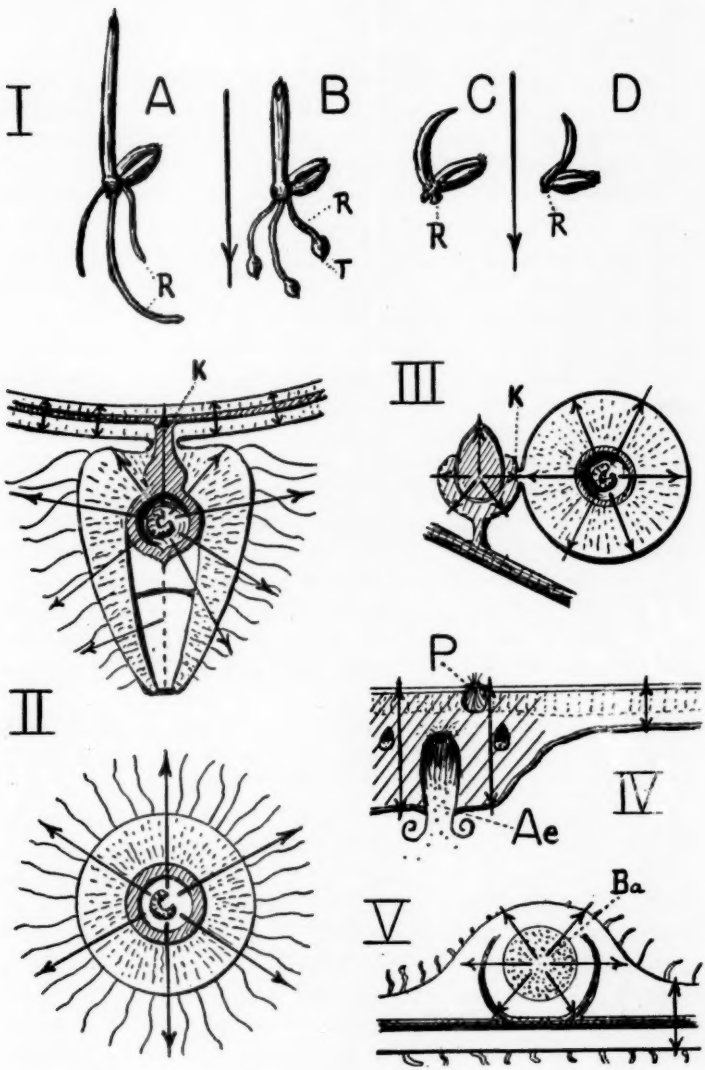


FIGURE 23.

c) Galls produced by Diptera, namely, by Cecidomyidae, are also open but more complex and involve deformations of buds and leaves, insuring better protection for larvae. In the gall parenchyma two regions are differentiated, the outer one being formed of larger cells. Mitoses remain normal, but nuclear hypertrophy is more accentuated than in Acarina galls; those Diptero-cecidia are thus intermediate between *a* and *b*.

Maresquelle shows that the gall-making process in (*c*) consists mainly of a combination of hypertrophy, producing a pad, and of local growth inhibition, provoking an invagination of the larva in cecidian tissues (180). In category (*a*) the initial attack is frequently localized on a smaller number of young cells (Fig. 23, II and III, K) which are incited to proliferate strongly and to give a cecidian blastema. In this case an entirely new set of morphogenetic physico-chemical gradients is produced on a spherical or cylindrical pattern centered on the larva: ionic gradients commanding the distribution of sclerified and conducting elements (210); redox gradients governing the accumulation of nutrients (237); hydration gradients also, gall tissues being usually more hydrated than normal ones; finally various chemical gradients manifested by accumulation of tannins, organic acids, anthocyanins, sugars (185), etc. On the adult gall the place of the tiny group of initial cells of the blastema is well indicated by the spot of insertion of the narrow peduncle of the gall on the plant organ (Fig. 23, II and III, K).

More than 1500 known species of insects and arachnids have found this successful way of insuring the future of their breed. "Gall insects", says Porter Felt (145), "live in a world of their own and they are past masters in the art of beguiling or compelling the host plant to provide food and shelter with a minimum expenditure of effort on their part". Man is very proud of the success he has gained with a partial mastering of the plant kingdom in order to secure his food; this success, however, is only child's play in comparison to the wonderful achievements of the gall-makers industry. As compared with the hard toil of the ploughman, the swift puncture of a plant by an insect is so light and yet sufficient to control the plant to a greater degree than ever cultivation could do.

At their highest degree of perfection, galls are "complex structures which at first sight seem unrelated to the tissues from which they have developed" (145). Porter Felt adds that "a cardinal

requirement is that the feeding must be so gauged as to stimulate growth without killing too many plant cells . . . . In some of the more highly developed galls, there is a close approximation to the seed and its structure, the gall maggot taking the place of the seed itself ".

Masterpieces of the gall-building world are probably the complex galls produced by cynipids on oak leaves, such as that of *Andricus sulfureus* on *Quercus arizonica* (145) (Fig. 23, II). Perhaps less striking but nonetheless interesting because of the perfectly concentric structure of their gradient field, are the acorn galls, such as that of *Amphibolips gainesi* (Fig. 23, III). The disparity of size between the gall and the acorn shows to what extent the insect diverts the resources of the plant for its own welfare.

Until recently the process of gall-making was not at all understood beyond the assertion that it could not be only a matter of physical action but that chemical agents must be involved. A great step was made with the discovery of the role played by ribonucleic acids in cell division. I. F. Lewis and L. Walton, studying the cone galls of witch hazel, have found that the stem mother of the gall-making aphid (*Hormaphis hamamelidis*) executes a series of about 150 stings on a circular area of 0.3 mm. diameter on the lower face of the young leaf. They note (170): " In stinging, the stylets of the insect inject minute drops of a material secreted by a pair of thoracic glands. This sting material contains a substance which produces crystalloids showing a characteristic reddish or purplish cast in many stains. Injection may be first made directly into the cytoplasm of epidermal and subepidermal cells and later into intercellular spaces in the parenchyma and phloem areas. In either case the crystalloids enter the nucleus and finally the nucleolus. In the area affected the middle lamella of the cells is dissolved, the cells dedifferentiate, undergo rapid multiplication and finally are redifferentiated and reoriented as gall cells rather than leaf cells. Cells directly stung or receiving sting material lie in all parts of the stung area. Wherever crystalloids are found cells containing them exhibit hyperplasia and hypertrophy. The cecidogenic crystalloids appear not to be capable of self propagation. Continued stinging is necessary during the formative life of the gall. If the stem mother dies or is removed, growth of the gall soon ceases ".

S. Taylor, studying the gall of *Aylax glechomae* L. on *Nepeta hederacea* (233), observes that: " Cytoplasm of nutritive cells in

the gall definitely contained more ribose nucleic acid than normal leaf cells but considerably less than apical and floral meristem cells. Larval gland cell cytoplasm showed a striking amount of this acid to be present. Possibly secretions from these gland cells may affect the nucleic acid cycle of the leaf cells, so as to induce mitoses and subsequent gall growth".

From the above observations it seems that the immediate cause of the gall-making process must be sought in the intra-cellular injection of mito-genetic substances, perhaps ribo-nucleic acids, influencing all gradients of cell division, cell enlargement and cell maturation [6]. Metabolic gradients are also greatly disturbed, as demonstrated by over-production of tannic acid, anthocyanins, gums or even sugars (honey-dew producing galls). This problem will occur again in the field of practical applications of gradient transformation.

All modifications of gradients that we have described so far are sudden modifications due to violent external influences. It will be interesting also to determine how plant gradients have been progressively modified through long periods of time, through slow alterations of internal factors, either progressively or by jumps, either spontaneously or incited by ambiance variations. In other words, the evolution of gradients must be now considered. It may enable us in the future to produce real man-made galls, or "anthropo-cecidia", for our own benefit.

Evolution and Gradients

The most primitive algae exhibit no histological gradients. In the Cyanophyceae, for instance, all cells are equivalent, with the exception of heterocysts, and no lasting gradation is perceptible from one to the other in their adult state; only the growing tip exhibits temporary differences. The same is true of the filamentous Chlorophyceae but with stronger intra-cellular gradients, indicated, for instance, in chloroplasts of *Spirogyra* or *Zygnema*. In unicellular genera, such as *Chlamydomonas*, intra-cellular gradients are also strongly marked. Even in green algae possessing true tissues, histological gradients may be absent. All cells in a thallus of *Monostroma* are equivalent, except for sexual elements.

A higher state of differentiation is reached in other algae. In the thallus of *Dictyoneurum* (Phaeophyceae) a transverse multi-

[6] Remote action remains possible: Houard observed that cell hypertrophy reaches its maximum not at the direct contact of the cecidogenic animal, but at some distance, on what he calls the "cecidogenetic circle" (198).

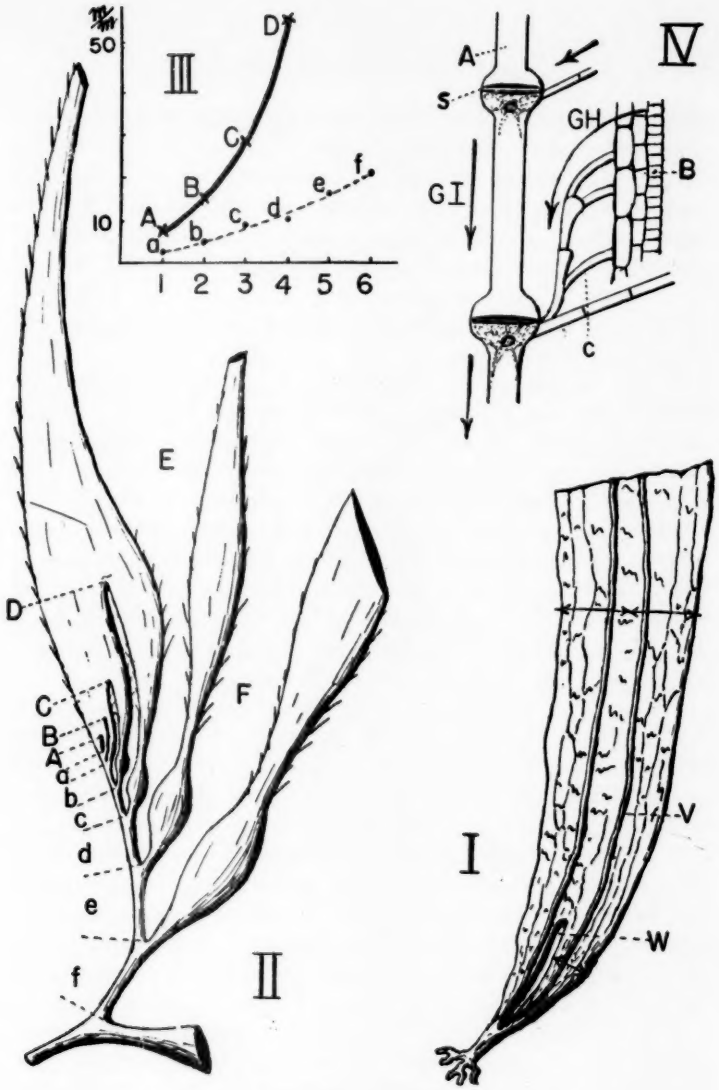


FIG. 24. Histological gradients in algae.

I. *Dictyonevrum californicum.* Birth of a transverse multinodal gradient, shown first by veins (V), then by fenestration (W).

II. *Macrocystis integrifolia.* A: region where a transverse gradient appears first in the tissues, determining fenestrations B, C, D in the apical part of the thallus and, later on, laciniations E, F.

III. Biometric gradations in *M. integrifolia.* Lengths of the internodes (a, b, c, d, e, f) are represented by the dotted curve, lengths of the windows (A, B, C, D) by the solid curve.

IV. Transition between intra-cellular gradient (GI) and histological gradient (GH) in *Asparagopsis.* A: big axial cells; B: photosynthetic elements; C: conducting elements; S: synapsis (143).

nodal gradient is well indicated, resulting in the differentiation of veins and windows, and finally in the splitting of the leaf (Fig. 24, I). In *Macrocystis* (Fig. 24, II) fenestration begins in the same way but is regularly repeated, ending in the multiple division of the frond (229). The steadiness of anatomical and morphological gradients in this genus is illustrated in Fig. 24, curves III showing the increase in length of internodes a, b, c, d, e, f and of windows A, B, C, D. Such a regularity is exactly comparable to that displayed by higher plants.

In the Rhodophyceae interesting cases of connection between intra-cellular and histological gradients can be detected. In *Asparagopsis* (Fig. 23, IV) Feldmann has shown a protoplasmic polarization related to the conduction role of the big axial cells (A) (143). The cytoplasm and the nucleus are concentrated at one extremity, a single big vacuole occupying the other end. Numerous small cells collect the products elaborated by photosynthetic tissues (B). True histological gradients can be observed through them, from chlorophyll cells (B) to axial cells (A), marked by progressive fragmentation of the vacuome, disappearance of rhodoplasts and increase in cell dimensions (143).

In mosses histological gradients are greater in the sporophyte than in the gametophyte. Inside the seta of the sporangium the gradients are often sufficient to result in differentiation of a true central cylinder with elongated cells imitating phloem and xylem elements. Higher up, in the capsule, histological gradients are clearly visible, resulting in differentiation of the sporogenous layer. The latter fact is in line with observations of J. H. Taylor showing that meiosis is determined by the establishment of chemical gradients inside growing tissues (232). The place of the sporogenous layer is probably marked by a local inflection of chemical and physiological gradients in the bulk of the young capsule.

Steep gradients, resulting in the production of highly differentiated tissues, are characteristic of archegoniate sporophytes. In the gametophyte, on the contrary, gradients are weaker, producing only feeble differentiation. H. Devaux has noted that aeriferous ducts are located only in the sporophyte as a result of a peculiar heteropolarity of molecules (133), while inside the gametophyte cells are stuck together or immersed in a jelly without aeriferous spaces (203). This observation might indicate a wide relationship between histological gradients and molecular heteropolarity.

In vascular plants consideration of gradient evolution could be almost endless (94, 95, 156, 203), and we shall therefore consider here only some peculiarly striking facts connecting evolution of gradients with plant morphogenesis. Let us compare, for instance, some species belonging to the great genus *Veronica*. In *V. spicata* and *V. spuria* flowering heavily affects the entire upper part of the stem, all the flower buds being clustered there and the base of the stem remaining entirely deprived of flowers. In these plants sexual gradients show a sharp rupture between the two parts of the axis, the inflorescence being an entity by itself, neatly separated from the vegetative base. In *V. hederaefolia* and *V. cymbalaria*, on the contrary, flowers are dispersed all along the stem in the axils of the leaves. There the sexual gradient is feebly expressed all along the axis. Such morphological differences are related to contrasts in the behavior of the axes toward geotropism; in the first case stems are strongly orthotropic, while in the second they are creeping. Thus is affirmed, once more, the intimate connection between physiological and anatomical gradients.

In *Linaria*, also of the Scrophulariaceae, it is possible to observe the same type of difference between species. *L. italica* and *L. vulgaris* present terminal inflorescences, dense and strongly orthotropic, with a sharp breaking of gradients between vegetative and sexual parts of the axis. In *L. cymbalaria* and *L. aequitriloba* the flowers, solitary and interspersed among the leaves on creeping stems, offer a " stagnant " type of gradient similar to the one of *V. hederaefolia*. Here appear striking illustrations of the phenomenon referred to by Duval Jouve as " parallel variations among congeneric types " (138). Other illustrations may be found in varieties of cereals and potatoes, the work of geneticists here being to select, among numerous variations appearing in their gradient systems, the most useful for economic purposes.

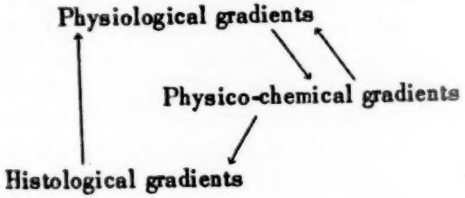
Carnivorous plants also offer interesting examples of gradients evolution. For instance, an urn of *Nepenthes* constitutes the most extraordinary field of contrasted gradients that can be imagined, from a plain uninodal histological gradient leading to the birth of a cavity at the tip of the central nerve of the leaf, to the tiny multinodal gradients producing rippled surfaces guiding the insect downward and forbidding it to climb back, and to the small concentric physiological gradients resulting in the differentiation of

digestive glands on the walls (181). Not less striking are the gradient systems of other carnivorous plants (*Dionea, Aldrovandia, Utricularia* (171)), where animal-catching apparatuses are again elaborated as greatly differentiated parts of the leaf.

What adjustments occurred in the ancestors of these highly specialized plants in regard of their morphogenetic gradients? At some time in the past those ancestors doubtlessly displayed a type of leaf deprived of all carnivorous mechanism, and they lived exactly in the same way as every other autotrophic plant. At that remote epoch, however, the tip of the midrib of their leaves already possessed the potentiality of producing insectivorous devices. The gradient system at the nerve tip was still homogeneous, but soon it was potentially capable of becoming complicated to develop those extraordinary insect lures. Perhaps in some millions of years the present insignificant tips of the leaf midrib of common plants around us will diversify to the point of producing surprisingly complicated apparatuses that we are presently unable to conceive. Careful observation alone of the processes through which the gradient systems of other plants evolved in the past to generate the present structures can enable us to foresee, to a certain extent, the possible directions of this future evolution and may permit us to orientate or to accelerate this evolution to man's advantage (211). The aforesaid recent results obtained in disturbing the gradient systems by toxic agents constitute the best proof that such possibilities are no longer a dream but are within our reach.

CONCLUSION

In the two parts of this memoir we have tried to present the complex subject of gradients in plants. In the first part (210) physico-chemical and physiological gradients have been described and their connections with growth (auxetic) gradients discussed. Correlations between them can be schematized as follows:



In the second part histological and anatomical gradients are examined, examples being chosen among grasses, pines, potatoes, etc. Dermograms of grasses have shown that some tissues strikingly reveal a network of isopotential lines giving evidence of the graded influences that govern their early differentiation.

Finally the most interesting and also the most difficult point of our study—modifications of the gradient system by external factors—was approached. The influence of chemical, physical and biotic agents is discussed, with reference to the amazing case of galls. If man becomes able to modify at will the gradients of a plant, he will be endowed with the ability to mould living matter according to his needs. At present hundreds of biologists are independently working on the subject of gradients in animals and plants. Coordination of their efforts and convergence of the latter toward detecting all means of modifying growth and metabolic gradients would open an unlimited new field of applications for the future welfare of mankind.

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